A study on the ecological significance of snow distribution in the low arctic tundra plant communities of Northern Fennoscandia

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A STUDY ON THE ECOLOGICAL SIGNIFICANCE OF SNOW DISTRIBUTION IN THE LOW ARCTIC TUNDRA PLANT COMMUNITIES OF NORTHERN FENNOSCANDIA

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DECLARATION

None of the material presented here has previously been submitted for a degree in this, or any other university. All of the work that is described is my own, except where stated otherwise.

James G. Cook

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ABSTRACT

A Study on the Ecological Significance of Snow Distribution in the Low Arctic Tundra Plant Communities of Northern Fennoscandia

James G. Cook

A combination of field/monolith-based experimentation and numerical modelling was used to study the short-term influence of snow distribution on various ecological/biogeochemical attributes of a range of contrasting Low Arctic tundra plant communities in northern Fennoscandia.

Experimental snow augmentation delayed the timing of snow melt, postponing early-season phenological development in a number of plant species, but had no effect on average plot greenness. Significant changes in stem growth, branching, leaf growth, leaf nutrient content, flowering and fruit production were also observed in response to the artificial increases in snow cover. The responses were generally species-specific and in many cases were also dependent on the type of community. Advanced snow melt was also found to exert a species-specific influence on plant phenology, promoting earlier occurrence of initial phenophases. Complete prevention of winter snow cover on the other hand, exerted a retarding influence on plant phenology.

Both increasing snow cover and removing it completely were found to reduce carbon turnover, but had negligible effects on net ecosystem CO_2 exchange. However, turnover and net CO_2 exchange were found to differ between communities, with model estimates suggesting that they were all CO_2 sources of varying strengths during the course of the study (although errors were large). The CO_2 model also demonstrated the importance of vegetation cover and phenology in determining annual ecosystem CO_2 balance. Snow melt date (independent of energy balance) was found to be less important.

The short-term effects of snow cover perturbation demonstrated here indicate a number of pathways by which snow may directly or indirectly (via modification of nutrient dynamics etc) influence the structure and functioning of tundra ecosystems. More detailed, long-term analysis is required however, to further elucidate the nature of these evidently crucial, yet complex snow-ecosystem interactions.

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CHAPTER 1: INTRODUCTION

1.1 BACKGROUND

On a global scale, snow plays a major role in the complex suite of interactive processes which determine the Earth's climate. Due both to the sensitivity of snow to temperature and its effect upon it (which results from its high albedo and thus its ability to influence the radiation balance (Bonan 2002)), the extent of global snow cover can provide a strong positive feedback to prevailing climatic conditions (Maxwell & Barrie 1989, Cess et al. 1991). Over millennia, snow also has a major impact upon the Earth's topography, the cyclic advance and retreat of glaciers reshaping the landscape through the formation of valleys and redistribution of substrates (Paterson 1969). Via these effects on climate and topography, snow can in turn exert a considerable influence upon the biosphere.

If we now consider the role of snow at a much finer spatial and temporal scale, the annual distribution and duration of snow cover within a landscape can influence its ecology in three main ways, interacting over decades to determine soil quality and community structure and composition (Gjærevoll 1956, Billings & Bliss 1959, Johnson & Billings 1962, Billings 1974, Ostler et al. 1982, Isard 1986, Evans et al. 1989, Sonesson & Callaghan 1991, Walker et al. 1993, Schaefer & Messier 1995, Jones 1999, Darmody et al. 2004, Löffler 2005, Callaghan et al. In Press).

Firstly, because snow is a good insulator (Bonan 2002), the snowpack can act as a blanket, protecting the vegetation underneath from the potentially damaging low temperature extremes and abrasive, desiccating winds of winter (Billings & Bliss 1959, Johnson & Billings 1962, Pruitt 1970, Billings 1974, Lewis & Callaghan 1976, Bell & Bliss 1979, Sonesson & Callaghan 1991, Sturm & Holmgren 1994, Scott & Rouse 1995, Jones 1999, Walker et al. 1999, Stieglitz et al. 2003, Aerts et al. 2004, Darmody et al. 2004, Rixen et al. 2004, Callaghan et al. In Press). With sufficient snow depth, soil temperatures may remain high enough for continuation of biological activity throughout the cold season (Schimel et al. 2004).

Secondly, the timing of snow melt can play a major role in determining when the growing season begins (Gjærevoll 1956, Billings & Bliss 1959, Holway & Ward 1965, Weaver & Collins 1977, Murray & Miller 1982, Ostler et al. 1982, Ram et al. 1988, Galen & Stanton 1991, Kudo 1991, Larigauderie & Kummerow 1991, Sonesson & Callaghan 1991, Woodley & Svoboda 1994, Walker et al. 1995,

Oberbauer et al. 1998, Price & Waser 1998, Hollister & Webber 2000, Rixen et al. 2001, Rixen et al. 2003, Rixen et al. 2004, Callaghan et al. In Press). The more snow that accumulates at a given location during the winter, the longer it will take to melt in the spring/early summer. Just as snow can insulate soil and vegetation against cold air temperatures in the winter, so it also inhibits their equilibration with warmer air temperatures in the spring. The ability of snow to delay warming of the soil and vegetation beneath it is further exaggerated by its high albedo, as mentioned above, which also reduces the amount of light received by the underlying vegetation, further inhibiting photosynthetic activity. In areas characterised by late-lying snow cover, the vegetation may not become snow-free until after the annual period of peak insolation (Lewis & Callaghan 1976).

Thirdly, the amount of snow that accumulates through the winter can considerably influence the hydrology of an area throughout the following snow-free period (Johnson & Billings 1962, Isard 1986, Scott & Rouse 1995, Kane 1996, Jones 1999, Dunne et al. 2003, Callaghan et al. In Press). As has been demonstrated by delta deuterium analysis (Welker et al. 1995), melt-water can be an important moisture input, especially in areas characterised by low precipitation.

Snow cover is ultimately dependent upon the quantity of snow that falls, but it is the interactive influence of wind, topography and vegetation structure that determines where this quantity is distributed within a landscape (Johnson & Billings 1962, Pruitt 1970, Billings 1974, Evans et al. 1989, Schaefer & Messier 1995, Kane 1996, Sturm et al. 2001a, Callaghan et al. In Press). Any snow that falls on sites exposed to the wind is typically scoured and redistributed in places where topography and/or vegetation provide shelter. Thus ridges tend to accumulate less snow than valleys, hollows or the leeward side of boulders, and sparsely vegetated areas tend to accumulate less snow than areas occupied by dense shrubs or forests. The temporal distribution of snow cover is in part determined by how much snow has accumulated, as influenced by the above factors, but also by those factors that control the rate of its removal from the landscape: Air temperature, solar radiation and wind. These factors are, in turn, also influenced by topography and vegetation.

Low Arctic (or Subarctic) tundra evades rigid, geographical classification, but can be generally defined on the basis of its climatic and ecological characteristics (Blüthgen 1970). It typically occupies the region lying between the northern extent of the

boreal forest and the discontinuous patch tundra of the High Arctic, experiencing low temperatures with a high degree of non-periodic variability, low precipitation, high winds and spatiotemporally heterogeneous seasonal snow cover (Blüthgen 1970). Conditions are generally sufficient for the production of continuous vegetation although considerable variability in productivity, due to heterogeneity in growing season length and microclimate, is a significant ecological criterion of the region (Blüthgen 1970, Hustich 1970). Floral diversity is typically low as a result of the adverse conditions, with only around 3% of the Earth's estimated plant species total occurring beyond the Arctic treeline (Callaghan et al. In Press); of these, the cryptogams are the best represented, accounting for 6.6% and 11% of all known bryophytes and lichens respectively. The region is also dominated by cold, wet, shallow soils, which restrict microbial decomposition of dead organic matter (Heal et al. 1981, Marion et al. 1997, Jonasson et al. 2000). Despite low productivity, over thousands of years, this has resulted in the accumulation of disproportionately large stores of organic material in these soils, accounting for a significant component of the global total soil carbon reservoir (Billings 1987, Billings & Peterson 1992, Wookey 2002, Callaghan et al. In Press).

Climate change, associated with a doubling in atmospheric greenhouse gas concentrations over the next 50 years, is expected to be greater in the Arctic than other regions due to feedbacks in which variations in snow and sea ice extent, ocean salinity, the stability of the lower troposphere and thawing of permafrost are likely to play key roles (Maxwell & Barrie 1989, Cess et al. 1991, Cattle & Crossley 1995, IPCC 2001, Sælthun & Barkved 2003, Kattsov et al. In Press, McBean et al. In Press). Over the past century, the Earth's climate has warmed by approximately 0.6°C with local increases as high as 2°C (Serreze et al. 2000, IPCC 2001). Although warming has not been uniform, land station measurements indicate that the Arctic has, on average, warmed by approximately 0.9°C during this time (McBean et al. In Press). General Circulation Model outputs suggest that over most Arctic land areas, mean annual temperatures will continue to increase over the next 100 years by a further 0.3 to 0.5°C per decade, with the greatest increases occurring during winter (Sælthun & Barkved 2003, Kattsov et al. In Press). It is also predicted that this warming will result in precipitation increases in the region of 5 to 35% (depending on location) by the end of the 21st century (Sælthun & Barkved 2003, Kattsov et al.

In Press). While this could result in increased snowfall through the winter and potentially delayed snowmelt, the associated increase in temperature might still lead to a considerably longer snow-free/growing season (Maxwell & Barrie 1989, Maxwell 1992, Sælthun & Barkved 2003, Førland et al. 2004). Indeed, despite increased autumn/winter precipitation in some regions, there is mounting evidence of a decline in the snow cover period of high latitudes over recent decades, due to advancement of spring snow melt in particular (Foster 1989, Robinson et al. 1993, Myneni et al. 1997, Serreze et al. 2000, Dye 2002, Dye & Tucker 2003, Kattsov et al. In Press, McBean et al. In Press).

Though the dynamics of snow-ecosystem interactions in the Low Arctic warrant the attention of scientific investigation in their own right, in light of the predicted changes in climate described above, and the powerful feedbacks that might ensue from any resulting changes in vegetation structure/composition and carbon turnover (Callaghan 1993, Moorcroft 2003, Callaghan et al. In Press, see Chapter 2), the need for a thorough understanding of the processes involved is ever more pressing.

1.2 THIS STUDY

1.2.1 Context and Objectives

This study was conducted as a part of STEPPS (Snow in Tundra Ecosystems: Patterns, Processes and Scaling); an interdisciplinary, Natural Environment Research Council funded research project with collaborators from the University of Durham, the Centre for Ecology and Hydrology at Wallingford, the Abisko Scientific Research Station and the University of Uppsala/Stirling. The aim of the STEPPS project was to investigate the influence of natural and artificially manipulated snow cover heterogeneity upon the ecology, hydrology, biogeochemistry and micrometeorology of a Low Arctic tundra fieldsite.

Having been designated the role of addressing a range of the ecological and biogeochemical elements of the STEPPS project, this study focused in particular on investigating the effects of different snow distributions upon plant development and ecosystem carbon dioxide exchange. In so doing, the study aimed to meet the following objectives:

1. To demonstrate how changes in the depth and duration of snow cover would affect the following ecological/biogeochemical parameters:
    a. Plant phenology
    b. Plant vegetative growth
    c. Plant reproductive output
    d. Gross primary productivity
    e. Ecosystem respiration
    f. Net ecosystem CO_2 exchange

2. To demonstrate how these effects would differ between:
    a. Species (where applicable)
    b. Communities
    c. Years

3. To demonstrate how the above parameters would naturally vary between:
    a. Communities
    b. Years

1.2.2 Approaches

A variety of techniques was employed to meet the above objectives:

1. An *in situ*, plot-based, snow manipulation experiment was conducted at the STEPPS fieldsite over two years commencing in September, 2002.

2. An *ex situ*, monolith-based, snow manipulation experiment was conducted at the Abisko Scientific Research Station over one year commencing in September, 2003.

3. CO_2 exchange was modelled for the study communities at the STEPPS fieldsite over 2003 and 2004.

1.2.3 Thesis Outline

Having provided here a brief background to the study and outlined its main objectives and the approaches used to meet them, the next chapter reviews the relevant literature on Arctic plant phenology, plant performance and ecosystem carbon dioxide exchange, with a particular emphasis on environmental influences, including snow cover. In the third chapter, the methods employed in the field and monolith experiments are described, the results of which are presented in chapters four and five respectively. Chapter six describes the modelling experiment and its results. In the final chapter, the results of both of the experiments and the modelling exercise are brought together and discussed in the context of the study objectives and the existing literature, followed by a summary of the study and its conclusions.

1.2.4 Nomenclature and Conventions

The scientific species names used in this study follow those given in Tutin et al. (1964, 1968, 1972, 1976, 1980). The English names follow those given in Grey-Wilson & Blamey (1995).

In reference to ecosystem carbon dioxide exchange, this study follows a micrometeorological convention whereby negative CO_2 fluxes represent an extraction of CO_2 from the atmosphere and positive fluxes, an addition of CO_2 to the atmosphere. Respiration values are therefore always positive and photosynthesis values, negative.

CHAPTER 2: LITERATURE REVIEW

2.1 ARCTIC PLANT PHENOLOGY

Plant phenological development is subject to a range of autonomous and environmental influences (Rathcke & Lacey 1985). The nature of these influences varies amongst phenophases, species and locations (Woodley & Svoboda 1994, Fitter et al. 1995, Henry & Molau 1997, Press et al. 1998a, Defila & Clot 2001, Molau et al. 2005), as does the extent to which the governing processes are understood. In the Arctic, the role of microenvironment in the regulation of plant phenology has long been appreciated (Sørensen 1941, Bliss 1956), as has the fact that certain species depend more upon such external cues than others (Sørensen 1941). Differences in the level of inter-site synchronicity between phenophases (Murray & Miller 1982) suggest that the relative importance of external cues may also vary within a single species from one phase to another.

Many studies have investigated the influences of various environmental factors on the phenology of Arctic plants. Much of this research has focussed upon the role of temperature (Jackson 1966, Heide 1992, Stenström & Molau 1992, Wookey et al. 1993, Woodley & Svoboda 1994, Alatalo & Totland 1997, Henry & Molau 1997, Jones et al. 1997, Lévesque et al. 1997, Molau 1997, Mølgaard & Christensen 1997, Shevtsova et al. 1997, Stenström & Jónsdóttir 1997, Suzuki & Kudo 1997, Welker et al. 1997, Press et al. 1998a, Thórhallsdóttir 1998, Arft et al. 1999, Hollister & Webber 2000, Karlsson et al. 2003, Aerts et al. 2004, Molau et al. 2005), a factor known to be of importance in the regulation of plant development, especially reproduction (Grainger 1939, Rathcke & Lacey 1985). The results of these studies concur that phenological development is accelerated by increasing air and soil temperatures in a range of growth forms at a variety of Arctic and alpine locations, with the greatest responses occurring in the High Arctic. While temperature-induced advancement of early season phenology has consistently been observed to increase the length of the active growing season, the role of temperature in determining end of season phenology is less clear cut, with some studies suggesting that higher air/soil temperatures do postpone the onset of foliar senescence (Woodley & Svoboda 1994, Walker et al. 1999, Marchand et al. 2004b), and others suggesting that they do not (Jones et al. 1997, Arft et al. 1999). This

reflects the poor extent to which the regulation of foliar senescence is currently understood (Noodén et al. 1997, Yoshida 2003).

As well as temperature, studies suggest that photoperiod (Holway & Ward 1965, Molau 1997, Häkkinen et al. 1998, Keller & Körner 2003), soil moisture (Holway & Ward 1965, Woodley & Svoboda 1994) and nutrient availability (Larigauderie & Kummerow 1991, Woodley & Svoboda 1994, Press et al. 1998a) can also influence the phenology of Arctic plants. In some cases, these factors may be more important than temperature in regulating the onset of dormancy at the end of the growing season (Shaver & Billings 1977).

In seasonally snow covered systems such as those that occur in the Arctic and in alpine areas, the depth, and to a greater extent, the duration, of the snow pack can have a profound influence on plant phenology by determining when light, moisture, nutrients and temperatures suitable for biological activity become accessible in the spring. In such systems, where snow cover restricts the length of the growing season, phenological development is typically rapid after snow release, with the timing of early-season phenophase occurrence at least, ultimately depending upon the timing of snow melt (Billings & Bliss 1959, Holway & Ward 1965, Weaver & Collins 1977, Murray & Miller 1982, Ostler et al. 1982, Ram et al. 1988, Galen & Stanton 1991, Kudo 1991, Larigauderie & Kummerow 1991, Woodley & Svoboda 1994, Walker et al. 1995, Oberbauer et al. 1998, Price & Waser 1998, Hollister & Webber 2000, Rixen et al. 2001, Rixen et al. 2003, Molau et al. 2005). The acceleration (or "telescoping") of plant phenology in areas of late snow melt is also well documented (Sørensen 1941, Billings & Bliss 1959, Ostler et al. 1982, Stenström & Molau 1992, Walker et al. 1999) and is probably attributable to the warmer temperatures experienced by plants emerging from the snow later in the growing season. As a consequence of this telescoping, the phenological synchronicity of sites with different snow cover regimes is likely to increase as the growing season progresses and the late-release sites effectively catch up. Not surprisingly, combinations of advanced snow melt and increased temperature have also been found to accelerate phenological development (Oberbauer et al. 1998, Price & Waser 1998, Starr et al. 2000, Dunne et al. 2003), although in some cases, reduced snow cover can delay reproductive phenology by increasing the exposure of plants to cold winter temperatures (Inouye & McGuire 1991). Where seasonal snow

cover is less restrictive, other factors such as temperature regain complete dominance over phenological control (Thórhallsdóttir 1998).

All of the factors discussed so far influence the phenology of Arctic plants both in the short-term, by providing the cues or necessary conditions for the advancement of vegetative and reproductive development, and also in the long-term, via the application of selective pressures which shape the evolution of the plants' life history strategies (Molau 1993). These long-term selective pressures can also operate indirectly via influences upon biotic variables such as the abundance of pollinators, seed predators and herbivores (Mosquin 1971, Inouye & McGuire 1991, Brody 1997). Where there is a high degree of spatiotemporal variability in evolutionarily influential environmental factors such as snow cover, fine tuned phenological adaptation may not be possible, or a range of adaptive strategies may co-occur (McGraw & Antonovics 1983, Jackson & Bliss 1984, Bishop & Schemske 1998). It has been argued that high variation in reproductive phenology may be a sign that it is not subject to strong selective pressure (Ollerton & Lack 2003); however, the common correlation of flowering time with seed set success would appear to suggest otherwise (Rathcke & Lacey 1985).

Across much of the Northern Hemisphere, the general trend in recent decades has been a lengthening of the active growing season, which has been associated with climatic warming. Changes in spring phenology are the most commonly reported (Sparks & Menzel 2002, Walther et al. 2002), with analyses of long-term phenological records revealing phenological advances of up to four weeks in parts of Europe since the 1950s/60s (Menzel & Fabian 1999, Defila & Clot 2001, Menzel et al. 2001, Ahas et al. 2002) and a concurrent phenological advancement reported for North America (Schwartz & Reiter 2000). Although such advances are by no means a universal phenomenon (Karlsson et al. 2003), satellite data do show an earlier springtime greening trend in high northern latitudes over the last two decades (Myneni et al. 1997, Dye & Tucker 2003, Stöckli & Vidale 2004, de Beurs & Henebry 2005). Changes in autumn phenology have not been so apparent (Menzel & Fabian 1999, Defila & Clot 2001, Sparks & Menzel 2002).

2.2 ARCTIC PLANT PERFORMANCE

The success of those relatively few species that are able to survive and propagate in the harsh environments that occur beyond the treeline in the Arctic is dependent upon the possession of a number of pre-adapted traits (Sonesson & Callaghan 1991, Callaghan et al. In Press). Typically these include a long-lived prostrate growth form with greater biomass allocated to belowground roots and storage organs than to shoots and leaves (Billings & Mooney 1968, Billings 1974, Sonesson & Callaghan 1991, Callaghan et al. In Press), the ability to resist extreme cold and function at low temperatures with lower optimal temperatures for photosynthesis (Billings & Mooney 1968, Billings 1974, Kimball & Salisbury 1974, Lewis & Callaghan 1976, Gauslaa 1984, Sonesson & Callaghan 1991, Semikhatova et al. 1992, Callaghan et al. In Press), enhanced uptake and efficient use of limited nutrients (Sonesson & Callaghan 1991, Jonasson et al. 2000, Callaghan et al. In Press) and the ability to resist drought via reduced rates of transpiration (Billings & Mooney 1968, Billings 1974, Lewis & Callaghan 1976). Growth is usually greatest towards the beginning of the growing season (Billings 1974, Semikhatova et al. 1992), with generally more investment overall, in growth than in reproduction (Billings & Mooney 1968, Heide 1992); although the importance of reproduction may increase in the High Arctic, where there is greater potential for propagule establishment (Wookey et al. 1993). Despite low reproductive investment, sexual reproduction does still occur. However, as a consequence of the short, variable growing seasons that characterise the Arctic, it may take multiple years to complete the process, with the initiation of flower bud formation often taking place in the year prior to flowering, meaning that reproductive success can be more dependent upon the previous growing season than on more recent environmental conditions (Sørensen 1941, Holway & Ward 1965, Billings & Mooney 1968, Blüthgen 1970, Billings 1974, Johnstone & Henry 1997, Brooker et al. 2001).

As with phenology, a large number of studies have investigated the influence of various environmental factors on Arctic plant performance, focussing for the greatest part on the influence of temperature. Many have reported vegetative responses to warming, in a range of growth forms at a variety of Arctic and alpine locations, such as increased growth (Bliss 1956, Callaghan et al. 1989, Callaghan et al. 1997, Jones et al. 1997, Mølgaard & Christensen 1997, Shevtsova et al. 1997,

Stenström & Jónsdóttir 1997, Suzuki & Kudo 1997, Welker et al. 1997, Press et al. 1998a, Press et al. 1998b, Arft et al. 1999, Hartley et al. 1999, Jonasson et al. 1999, Walker et al. 1999, Hollister & Webber 2000, Bret-Harte et al. 2001, de Valpine & Harte 2001, Rustad et al. 2001, Marchand et al. 2004b, Sullivan & Welker 2005), changes in shoot architecture (Shevtsova et al. 1997) and increases in leaf C:N ratio (Welker et al. 1997). Increases in reproductive output and success in response to warming have also been commonly reported (Billings & Mooney 1968, Wookey et al. 1993, Alatalo & Totland 1997, Henry & Molau 1997, Johnstone & Henry 1997, Molau 1997, Molau & Shaver 1997, Mølgaard & Christensen 1997, Stenström & Jónsdóttir 1997, Welker et al. 1997, Press et al. 1998a, Arft et al. 1999, de Valpine & Harte 2001, Totland & Alatalo 2002).

While temperature is considered to be the most limiting factor to plant performance in the High Arctic (Havström et al. 1993, Henry & Molau 1997), nutrients appear to be the primary source of limitation at lower latitudes (Tissue & Oechel 1987, Nadelhoffer et al. 1991, Havström et al. 1993, Parsons et al. 1995, Press et al. 1998b, Robinson et al. 1998, Shaver et al. 1998, Graglia et al. 2001, Dormann & Woodin 2002, Richardson et al. 2002, Boelman et al. 2003, van Wijk et al. 2003a). The largest influence of temperature on Low Arctic plant performance may therefore be indirect, via its impact on the soil microbial processes controlling the availability of nutrients (Hobbie & Chapin 1998, Hartley et al. 1999, de Valpine & Harte 2001, Rustad et al. 2001, Dormann & Woodin 2002, Schimel et al. 2004), at least in those plants that have roots. Similar to temperature increases, nutrient additions have been found to induce increases in plant growth (Jonasson 1992, Parsons et al. 1994, Wookey et al. 1994, Parsons et al. 1995, Shaver & Laundre 1997, Press et al. 1998a, Press et al. 1998b, Shaver et al. 1998, Jonasson et al. 1999, Bret-Harte et al. 2001, Graglia et al. 2001, Bret-Harte et al. 2002, Gough & Hobbie 2003, van Wijk et al. 2003a, Hobbie et al. 2005) and reproductive output (Wookey et al. 1993, Wookey et al. 1994, Parsons et al. 1995) in numerous instances. Other factors that can influence nutrient cycling and availability, such as herbivory (Olofsson et al. 2004) and UV-B radiation (Gehrke et al. 1995, Zepp et al. 1998), may also therefore, have considerable indirect effects on Arctic plant performance.

As well as temperature and soil nutrient availability, other environmental variables such as atmospheric CO_2 concentration and UV-B radiation have also been found to have small direct effects on the performance of Artic plants (Johanson et al.

1995, Gwynn-Jones et al. 1997, Beerling et al. 2001). Biotic factors are also considered to play a role; the availability of pollinators for example, is a potentially fundamental limitation to plant reproductive success (Billings 1974, Stenström & Molau 1992, Kudo & Suzuki 2002).

The profound influence of snow on Arctic plant performance is clearly demonstrated by the sparseness of vegetation occurring in locations at either extreme of the snow cover continuum. Areas characterised by very late lying snow (and severely restricted growing seasons) or no snow at all (and extreme frosts, wind abrasion and desiccation) are both typically only colonised by cryptogams (Gjærevoll 1956, Billings 1974), although these contrasting environmental extremes are characterised by different species. The response of plant performance to changes in snow cover is therefore likely to depend on the position of each particular plant's location on the snow cover continuum.

A number of studies have described the reduction in plant size and productivity associated with late lying snow and restricted growing season length (Sørensen 1941, Billings & Bliss 1959, Holway & Ward 1965, Callaghan 1974, Weaver & Collins 1977, Ostler et al. 1982, Wijk 1986, Benedict 1990, Kudo 1992, Callaghan et al. 1997, Totland & Alatalo 2002), as well as decreases in plant reproductive output and success (McGraw & Antonovics 1983, Galen & Stanton 1991, Kudo 1991, 1992, Galen & Stanton 1993), with some shifts in life history strategy (Kudo 1991) and increases in negative plant-plant interactions also reported (Olofsson 2004, Totland et al. 2004). However, in other situations, increasing snow cover has also been found to have positive effects on Arctic plant growth (Bliss 1956, Scott & Rouse 1995, Walker et al. 1999, Sturm et al. 2001a, Dorrepaal et al. 2003, Sturm et al. 2005, Wahren et al. 2005) and either neutral (Totland & Alatalo 2002) or positive effects (Inouye & McGuire 1991, Aerts et al. 2004) on reproductive output and success, as well as apparently reduced levels of plant competition (Dietz et al. 2004). Increased snow cover may also have a positive influence on Arctic plant performance indirectly via its influence on nutrient availability. Although snow is not considered to be a direct major source of nutrients to Arctic plants (Brooks et al. 1996, Bilbrough & Welker 2000), by insulating soils in the winter, it can increase nutrient availability via the promotion of soil microbial activity (Schimel et al. 2004). This concurs with findings that increased snow cover

can lead to reduced C:N ratios in the leaves of Arctic plants (Henry & Molau 1997, Walsh et al. 1997, Welker et al. 2005).

The contrasting reports above support the notion that Arctic plant performance responses to snow cover change are dependent on the existing snow cover regime (depth and timing) and other factors, including the level to which the plant species' phenologies are synchronised with snow melt (Kudo 1992, Galen & Stanton 1995), soil moisture regime (Knight et al. 1979, Walker et al. 1995, Wahren et al. 2005), nutrient availability (Walker et al. 1995) and temperature (Walker et al. 1995, Heegaard 2002). This may at least partly explain why plant responses to short-term manipulations of snow cover might not reflect patterns observed in long-term, natural snow cover gradients (Galen & Stanton 1995).

There is much evidence that the response of Arctic plant performance to the various environmental variables discussed above is highly species specific (Chapin & Shaver 1985, Jonasson 1992, Parsons et al. 1994, Woodley & Svoboda 1994, Chapin et al. 1995, Harte & Shaw 1995, Potter et al. 1995, Scott & Rouse 1995, Chapin et al. 1996, Henry & Molau 1997, Suzuki & Kudo 1997, Molau & Alatalo 1998, Press et al. 1998b, Arft et al. 1999, Walker et al. 1999, Cornelissen et al. 2001, de Valpine & Harte 2001, Gorsuch et al. 2001, Graglia et al. 2001, Wipf et al. 2002, Brooker & van der Wal 2003, van Wijk et al. 2003a, Lesica & McCune 2004, Hollister et al. 2005, Wahren et al. 2005), with many studies reporting shifts in plant community composition in response to perturbation of these variables. There is also mounting evidence of the importance of timescale, as longer term studies begin to reveal contrasts between short and long-term plant-environment interactions (Chapin et al. 1995, Parsons et al. 1995, Arft et al. 1999, Hartley et al. 1999, Hollister et al. 2005).

Shifts in Arctic-alpine plant ranges and abundance in recent decades are indicative of long-term, individualistic alterations in plant performance. Reported shifts to date, include tree line migrations to higher latitudes and altitudes (Serreze et al. 2000, Kullman 2002), the disappearance of Arctic-alpine species from the lower margins of their latitudinal and altitudinal ranges (Grabherr et al. 1994, Lesica & McCune 2004) and increased shrub abundance/greenness at high latitudes (Serreze et al. 2000, Sturm et al. 2001b, Jia et al. 2003). Surprisingly, southward displacement of the tundra-taiga boundary has also been observed in some areas (Vlassova 2002,

Crawford et al. 2003), reflecting the complex nature of interactions between climate and the plant environment, as well as the confounding influences of human activities.

2.3 ARCTIC ECOSYSTEM CARBON DIOXIDE EXCHANGE

Despite their low metabolic temperature optima, the photosynthetic activity of Arctic plants is still temperature-limited most of the time (Semikhatova et al. 1992); although cryptogams, which generally have the lowest temperature optima for photosynthesis, may be more limited by moisture status (Lewis & Callaghan 1976, Schipperges 1992, Tenhunen et al. 1992). In terms of annual carbon assimilation, Arctic plants are also restricted by the limited window of opportunity for photosynthesis provided by the short growing seasons (White et al. 1999), a restriction that cannot even be compensated for by continuation of photosynthesis through the extended daylight hours of summer (Lewis & Callaghan 1976, Semikhatova et al. 1992), or advanced initiation of photosynthesis under shallow snow covers in the spring (Kimball & Salisbury 1974, Starr & Oberbauer 2003). These limitations on the rate and duration of photosynthetic activity are reflected by the small amounts of CO_2 typically sequestered by terrestrial Arctic ecosystems each year compared with other biomes (Lewis & Callaghan 1976, Wookey 2002). As ecosystem respiration is also constrained by low temperatures and short growing seasons however, as well as periodically anoxic soil conditions (Heal et al. 1981, Marion et al. 1997, Jonasson et al. 2000), emissions of CO_2 are also typically small.

Recent estimates of annual CO_2 exchange in different Arctic tundra ecosystems, derived from various combinations of field observations and modelling techniques, range from sink activity in the region of -194 g CO_2 m^{-2} yr^{-1} to source activity of approximately 660 g CO_2 m^{-2} yr^{-1} (Oechel et al. 1995, McKane et al. 1997, Oechel et al. 2000, Welker et al. 2000, Aurela et al. 2004, Mack et al. 2004, Welker et al. 2004). Overall, the average pan-Arctic CO_2 balance has been estimated to presently constitute a sink of -62 g CO_2 m^{-2} yr^{-1} with a standard deviation of 146 g CO_2 m^{-2} yr^{-1} (McGuire et al. 2000). However, there is currently too little data to ascertain whether the region is actually acting as an overall source or sink to atmospheric CO_2 (Callaghan et al. In Press). Whatever the net direction, most CO_2 exchange occurs during the growing season, although, as many have now

demonstrated, winter CO_2 emissions may also make a significant contribution to the annual CO_2 balance (Sommerfeld et al. 1993, Zimov et al. 1993, Oechel et al. 1996, Zimov et al. 1996, Fahnestock et al. 1998, Mast et al. 1998, Hobbie et al. 2000, Schadt et al. 2003, Aurela et al. 2004, Welker et al. 2004). During the growing season, the spatial variations observed in CO_2 exchange at the landscape scale are largely determined, among other things, by heterogeneity in the structure and composition of the vegetation (Grogan & Chapin 1999, Christensen et al. 2000, McFadden et al. 2003, Nykänen et al. 2003). Seasonal variations are also largely governed by vegetation, with rates of both uptake and efflux reflecting the progress of plant phenological development (Vourlitis 1999, Yuste et al. 2004).

As with phenology and plant performance, numerous studies have investigated the effects of various environmental factors on Arctic ecosystem CO_2 exchange. Again, many of these studies have looked at the effects of warming. Increases in net ecosystem CO_2 efflux/decreases in net assimilation resulting from proportionally greater responses of ecosystem respiration than photosynthesis to increases in soil and air temperatures have been frequently reported (Billings et al. 1982, Oberbauer et al. 1992, Oechel et al. 1995, Christensen et al. 1997, Christensen et al. 1998, Goulden et al. 1998, Jones et al. 1998, Shaver et al. 1998, Saleska et al. 1999, Welker et al. 1999, Welker et al. 2000, Mertens et al. 2001, Heikkinen et al. 2004, Jonasson et al. 2004). Other studies however, have reported that warming enhances ecosystem respiration and photosynthesis to the same extent, thus increasing the rate of carbon turnover, but having no overall impact on net ecosystem CO_2 exchange (Johnson et al. 1996, Hobbie & Chapin 1998, Marchand et al. 2004a). The nature of the response to warming is likely to depend on the existing soil moisture regime (Oechel et al. 1995, Welker et al. 2004), as this factor has also been found to affect Arctic ecosystem CO_2 exchange (Billings et al. 1982, Oberbauer et al. 1992, Johnson et al. 1996, Christensen et al. 1998, Saleska et al. 1999), but is itself partially dependent on temperature.

Similarly, temperature may have a major indirect influence on Arctic ecosystem CO_2 exchange via its effect on soil microbial activity and hence, nutrient availability (Melillo et al. 1993). As was mentioned in the previous section, Arctic plant growth is largely nutrient-limited. It is perhaps not surprising therefore, that associated with plant growth increases in response to nutrient addition, studies have found concurrent increases in plant carbon assimilation and hence, overall reductions

in net ecosystem CO_2 exchange (Billings et al. 1984, Christensen et al. 1997, Shaver et al. 1998, Johnson et al. 2000), more as a result of increased leaf area than enhanced photosynthetic capacity *per se* (Press et al. 1998a, Marchand et al. 2004a). Although, in some cases, respiratory enhancement was found to be as great (Illeris et al. 2004), or greater (Mack et al. 2004), than the increase in assimilation. This may be due to associated increases in litter production and changes in litter quality providing a greater source of utilisable carbon to decomposers (Nadelhoffer et al. 1991, Brooks et al. 2004, Jonasson et al. 2004, Loya et al. 2004), as microbial activity is thought to depend more upon recently fixed carbon near to the soil surface than the deeper bulk carbon stores (Christensen et al. 1999, Grogan et al. 2001, Grogan & Jonasson 2005). In the long-term therefore, direct responses of ecosystem CO_2 exchange to changes in temperature could potentially be modified by associated alterations in nutrient cycling and availability (Callaghan 1993, Oechel et al. 2000, Stieglitz et al. 2000, Oechel & Vourlitis 2003, Weintraub & Schimel 2005), not to mention any changes in community structure and composition that might also occur (Hobbie 1996, Gough & Hobbie 2003, Welker et al. 2004, Weintraub & Schimel 2005).

Through its effects on growing season length, microclimate and soil moisture/nutrient status, seasonal snow cover is likely to exert considerable influence over the CO_2 exchange of Arctic and alpine ecosystems. In some cases, ecosystem CO_2 assimilation has been found to increase with advanced snow melt (Harazono et al. 2003, Aurela et al. 2004), while in others, alterations in temporal exchange patterns and turnover rates were observed, but no overall change in net CO_2 balance (Oberbauer et al. 1998, Saleska et al. 1999). Increasing the depth and duration of snow cover has also been found to result in more negative values of net growing season CO_2 exchange, although these responses were additionally dependent upon temperature and moisture regime (Jones et al. 1998, Welker et al. 2000). Winter CO_2 efflux on the other hand, has been found to increase with greater snow depth, due to the enhancement of respiratory activity associated with superior insulation (Brooks et al. 1997, Fahnestock et al. 1998, Mast et al. 1998, Walker et al. 1999, Welker et al. 2000), although this has not proven to be a universal phenomenon either (Jones et al. 1999). Nevertheless, the influence of snow cover on winter soil temperatures and freeze-thaw dynamics in the autumn and spring are likely to play a major role in the determination of net ecosystem CO_2 exchange (Brooks et al. 1997,

Bubier et al. 2002), especially so considering the enhanced sensitivity of frozen soils to changes in temperature in comparison to non-frozen soils (Mikan et al. 2002).

CHAPTER 3: MATERIALS AND METHODS

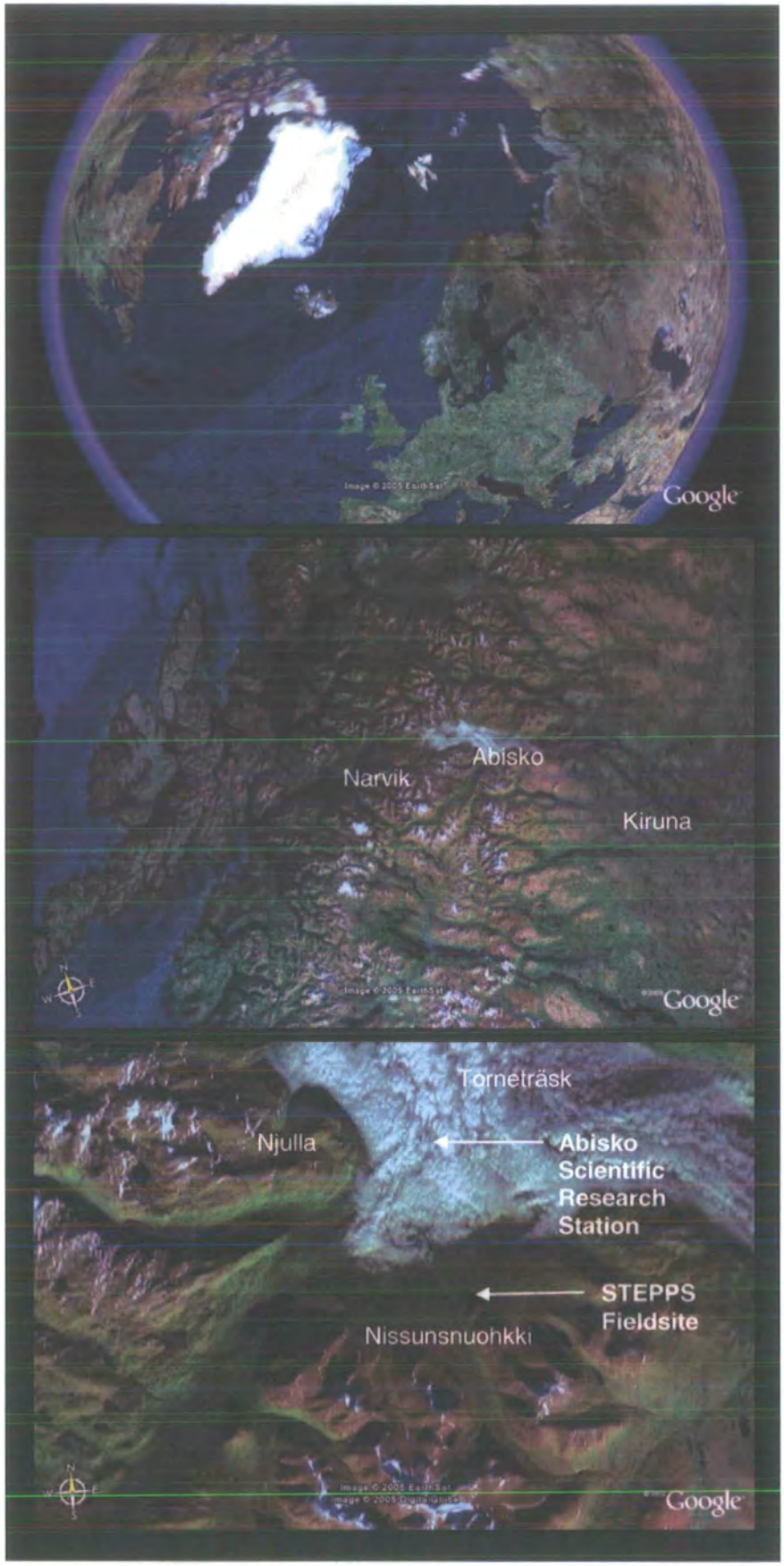

Figure 3-1: Satellite images showing the location and the surrounding geography of the Abisko Scientific Research Station and the STEPPS fieldsite.

3.1 THE FIELD EXPERIMENT

3.1.1 Site Description

The field experiment was conducted at the STEPPS fieldsite, approximately 7 km south of Abisko, northern Sweden (Grid Ref: 68°18'N 18°51'E; see Figure 3-1 and Figure 3-2). The site is spread over an area of roughly 1.5 km^2 on the northern flank of Nissunsnuohkki, between 700 and 780 m above sea level.

Situated at the northern end of the Scandinavian mountain chain, the landscape is dominated by rounded peaks of 1000 to 2000 m divided by broad U-shaped glacial trough valleys. Bound by steep scree slopes that climb up to the south and the Nissunjohka canyon to the west, the fieldsite occupies the top section of a gentle slope (c.a. 5°) that extends gradually down towards Lake Torneträsk in the north. The slope's gentle inclination is however broken into terraces by a network of steep sided ridges and hollows that follow the contours of the mountainside. At a smaller spatial scale, the topography of the site is further enhanced by numerous periglacial patterned ground formations.

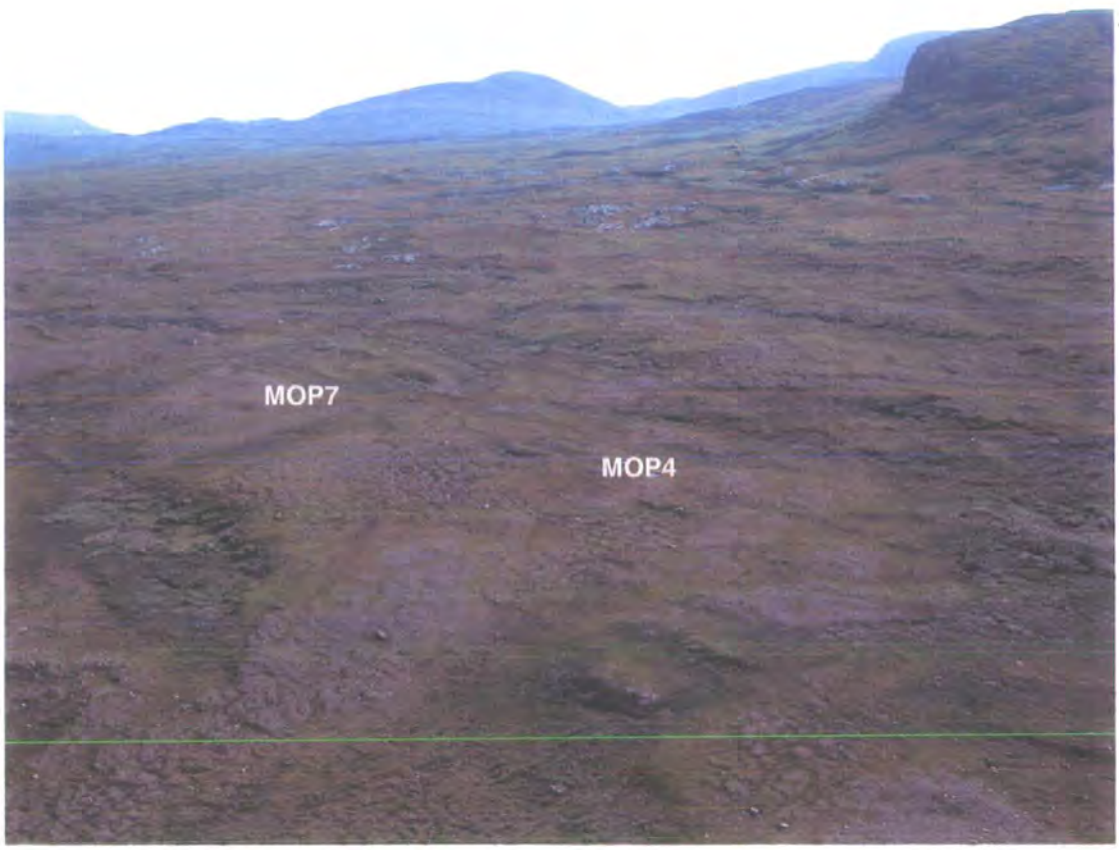

Figure 3-2: Aerial view of the STEPPS fieldsite and surrounding tundra; July, 2003. The locations of two of the meteorological observation points are also given (see section 3.1.3).

The climate of the area is subject to both continental and oceanic influences, further modified by the mountainous topography and the presence of Lake Torneträsk. Although there are no long-term climate data for the fieldsite itself, the meteorological record from the Abisko Scientific Research Station gives some idea of typical conditions in the same general area (although it is important to bear in mind that the fieldsite is approximately 400 m higher than the research station and therefore, is typically ~2.6°C cooler; assuming an atmospheric lapse rate of 6.5°C km^{-1}). Due to the high latitude and alpine terrain, the amount of incoming solar radiation varies greatly from one season to the next; peaking in June with round the clock sunlight, solar radiation drops to zero from mid-November through until the end of January, during which time the sun fails to rise above mountains that line the horizon. In Abisko, daily average air temperatures usually range between -32 and +22°C, with an annual mean of -0.5°C (for 1971 to 2000). Precipitation is significantly lower than in the nearby mountains to the west, with an average of 318 mm falling each year (for 1971 to 2000). From October through until June much of this falls as snow. The fieldsite itself is very exposed and is therefore subject to high winds, prevailing from the southwest with gusts in excess of 20 m s^{-1} not uncommon. Throughout the long Arctic winter these winds continually redistribute the snow across the landscape, scouring the exposed ridges and forming deep drifts of compacted wind-slab in the more sheltered areas. The timing of snow release in the spring/early summer is therefore highly variable, with some patches completely snow-free by March, and others still covered as late as June. Owing to the strong influence of snow distribution, soil temperature and soil moisture are in turn, accordingly variable from one patch to the next.

Sandwiched between the upper limits of the mountain birch forest (*Betula pubescens* ssp. *tortuosa*) and the sparsely vegetated moraines of the mountain's upper slopes, the fieldsite is populated by a complex mosaic of tundra plant communities, reflecting the high level of environmental heterogeneity. The sheltered hollows, characterised by greater snow accumulation in the winter, subsequent longer duration of snow cover in the spring and higher soil moisture contents throughout the growing season, tend to be dominated by larger shrubs such as *Salix glauca, Salix lanata, Betula nana* and *Juniperis communis* and have a rich field layer containing dwarf shrubs such as *Vaccinium myrtillus* and *Phyllodoce caerulea* and a variety of herbs including *Trollius europaeus*, *Solidago virgaurea*, *Viola biflora*,

Potentilla crantzii, *Thalictrum alpinus*, *Saussurea alpina* and *Linnaea borealis*. At the other extreme, the exposed ridges, characterised by little or no winter snow cover and very dry soils during the growing season, are only sparsely vegetated by higher plants. Above the diverse crust of lichens and bryophytes, the most abundant species tend to be dwarf shrubs (in prostrate form) such as *Empetrum hermaphroditum, B. nana, Vaccinium uliginosum* and *Diapensia lapponica*. A series of intermediate communities (both in structure and composition) occupy those areas between ridge and hollow, mostly consisting of *E. hermaphroditum/B. nana*-dominated heath, with sedge dominated vegetation (including *Carex vaginata*, *Eriophorum vaginatum* and *Trichophorum cespitosum*) occupying the wetter patches and species such as *Andromeda polifolia*, *Arctostaphylos alpinus*, *Rhododendron lapponicum*, *Cassiope tetragona*, *Dryas octopetala*, *Loiseleuria procumbens* and *Tofieldia pusilla* occurring throughout.

3.1.2 Experimental Design

Although the spectrum of plant communities present at the field site could be divided into many different classes, for the purposes of this study the vegetation has been grouped into four broad categories that incorporate the most abundant elements of the mosaic, representing a broad range of environments in terms of winter snow cover and soil moisture status (see Table 3-1).

Table 3-1: The original study communities and their characteristics.

Name	Dominant Growth Forms	Vegetation Height (cm)	Winter Snow Depth (cm)	Soil Moisture Status
Fen	Graminoids/bryophytes	0-10	5-20	Wet
Heath	Dwarf shrubs	5-20	5-30	Dry-Mesic
Hollow	Shrubs/herbs	5-120	30-200	Mesic-Wet
Ridge	Cryptogams/prostrate dwarf shrubs	0-5	0-15	Dry

In each of the four communities, the effects of four different snow scenarios were to be tested:

1. "Normal", unmanipulated snow cover (control)
2. Increased snow cover (+snow)
3. Accelerated snow melt (+melt)
4. Increased snow cover and accelerated snow melt (+snow+melt)

Each treatment was to be replicated five times in each of the four communities with the exception that no '+snow' treatment was to be implemented in the Hollow community, due to the difficulty of increasing snow accumulation beyond that which occurs naturally, and no '+melt' treatment was to be implemented in the Ridge community, due to the scarcity of the snow cover that occurs there naturally. With the exception of the Hollows and the Ridges, the layout of the experiment would follow a randomised block design with five complete replicate sets of all four treatments in five different, similarly vegetated, randomly selected patches per community (20 patches in total). However, in the spring of 2003 it became apparent that, like the Ridges, there was insufficient snow cover to implement the '+melt' treatment in the Heath and Fen communities.

The '+snow' treatment was implemented passively via the construction of 15 snowfences (five in each of the three communities receiving this treatment) (see

Figure 3-3: One of the 15 snowfences at the STEPPS fieldsite; February, 2003.

Figure 3-3). Each snowfence consisted of two L-shaped sections of plastic, latticed fencing material secured with posts of iron reinforcement-bar, arranged to form a cross aligned with the four cardinal points of the compass. Each arm of the cross measured 3 m from the centre and stood 1.2 m tall. During the winter, snow accumulated on the sheltered, leeward side of the fences (in this case, the northeast quadrants), allowing the formation of a deeper snow-pack than that which would occur naturally.

The '+melt' treatment was also to be implemented passively, this time by securing 4×4 m sheets of black, plastic-weave material to the snow surface. It was predicted that the black sheets would absorb more solar radiation than an unmanipulated, high albedo snow surface. The increased solar energy input would then be transferred as heat to the snow-pack below, thus accelerating the rate at which it melted. The '+snow+melt' treatment was to be implemented by placing the black sheets on areas of increased snow cover created by the snowfences.

Despite considerable efforts, the black sheet method was found to be incapable of producing the desired acceleration of snow melt. In consequence, all '+melt' and '+snow+melt' treatments had to be omitted from the field experiment. In the Hollows this left only the control treatment, so this community was completely excluded.

A 2×2 m plot was established in each of the remaining treatment replicates in each of the three remaining communities (see Figure 3-4). The plots were marked out with a short, white, plastic section of tubing driven into the ground in each corner. A longer, orange, plastic, roadside marker pole was also inserted in the vicinity of each plot to render them conspicuous in all weather conditions. Using the methods described in the following sections, plant phenology, plant performance and ecosystem CO_2 exchange were subsequently monitored within each plot throughout the snow-free periods of 2003 and 2004.

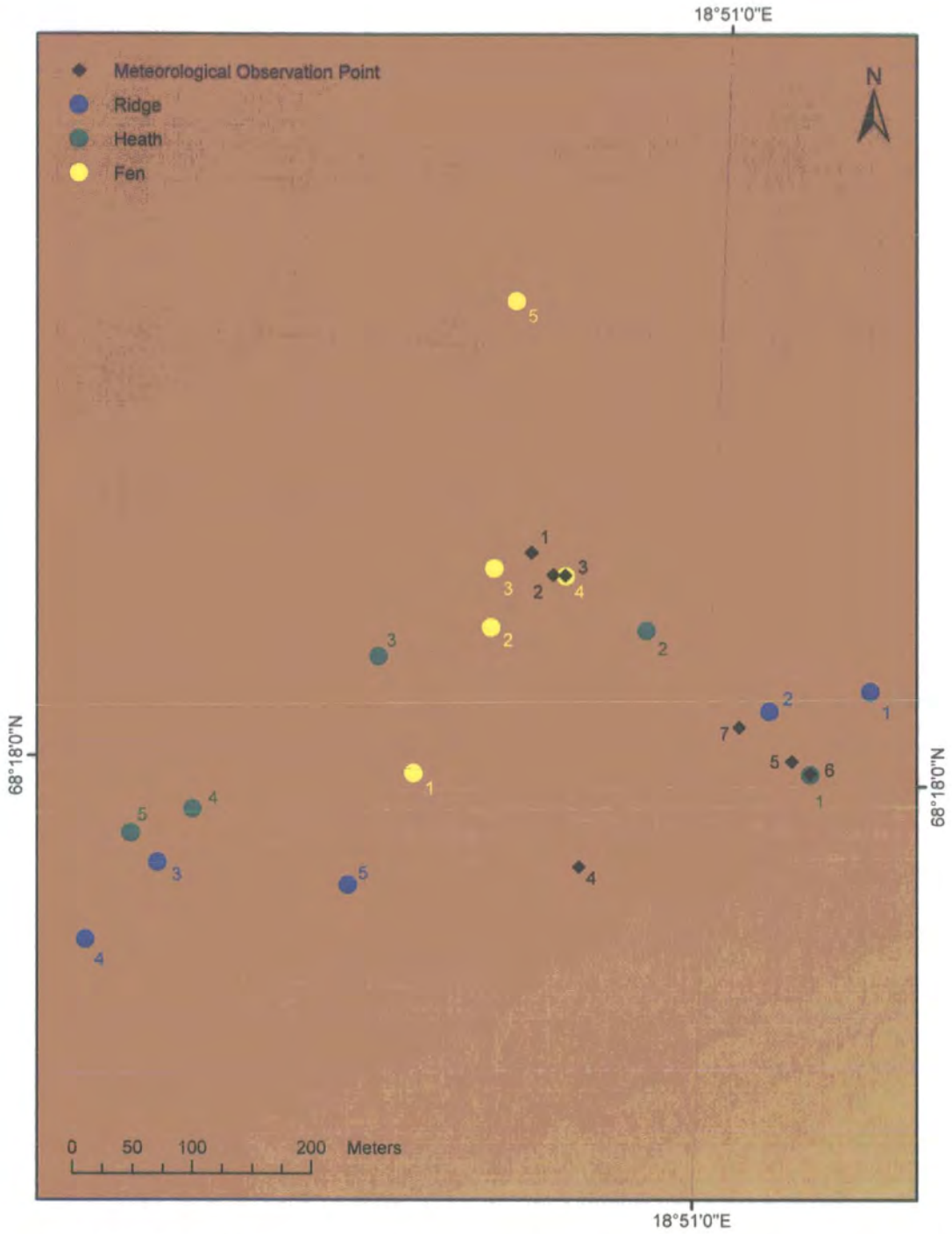

Figure 3-4: Map of the STEPPS fieldsite showing locations of study plots and meteorological observation points. Each of the Fen, Heath and Ridge symbols represents a pair of plots, one 'control' and one '+snow'. There are five replicate pairs in each of the three communities, giving a total of 30 plots.

3.1.3 Abiotic Parameters

Six abiotic parameters were of particular relevance to this experiment:

1. Snow depth
2. Timing of snow melt
3. Soil temperature
4. Soil moisture
5. Air temperature
6. Solar radiation

Values for these parameters were obtained for each treatment/community, where possible, from the automatic instrumentation deployed at a selection of the eight meteorological observation points (MOPs) at the STEPPS fieldsite (instruments were deployed by C.R. Lloyd, R. Baxter, A. Fox and R. Harding) (see Table 3-2, Figure 3-4 and Figure 3-5). Where this was not possible and/or individual plot values were required, manual observations were made.

Table 3-2: MOP locations.

MOP	Community	Treatment
1	Fen	control
2	Fen	control
3	Fen	+snow
4	Heath	control
5	Heath	control
6	Heath	+snow
7	Ridge	control
8	Ridge	+snow

Snow depth was measured automatically throughout the study period at MOPs 1, 3, 4, 6, 7 and 8 with SR50 acoustic distance sensors (Campbell Scientific Ltd, Leicestershire, UK). The sensors were suspended up to 2 m above the ground on aluminium frames and snow depth calculated as the difference between the distance from the sensor to the surface below, as measured by the sensor, and the actual distance from the sensor to the ground (without snow). Each sensor was

Figure 3-5: An automatic weather station at the STEPPS fieldsite (MOP1); February, 2003.

connected to a CR10X datalogger (Campbell Scientific Ltd, Leicestershire, UK) which recorded half-hourly averages of snow depth.

Manual snow depth surveys were also conducted around the time of peak snow accumulation at the end of March in both 2003 and 2004. In each case, an aluminium snow probe was used to measure snow depth at five random points within each plot so that plot averages could be calculated. During the 2003 snow depth survey, the snowfence drifts were also measured. For each snowfence, snow depths were recorded at 1 m intervals across a grid that encompassed the entire drift.

The timing of snow melt was recorded manually for each of the study plots in 2003 and 2004. In both years the plots were surveyed at regular intervals from March until they were all completely snow-free. During the surveys, each plot was given a snow cover index score from one to four according to the extent to which they were snow covered (see Table 3-3). This method was deemed more suitable than measuring the snow depth at each plot, as it accounted for sub-plot heterogeneity in the timing of snow release.

Table 3-3: Key to snow cover index scores.

Snow Cover Index	Percentage Snow Cover
1	>90% snow covered
2	50-90% snow covered
3	10-49% snow covered
4	<10% snow covered

Soil temperature was measured automatically throughout the study period at MOPs 2, 3, 5 and 6 at depths of approximately 5 cm using custom made thermocouple ring frost gauges (CEH Wallingford, UK) connected to CR10X dataloggers which recorded half-hourly averages. In the Ridge communities however, the ground was too stony for the insertion of such large probes. Therefore, at MOP7 soil temperature was measured at 5 cm using a 107 thermistor probe (Campbell Scientific Ltd, Leicestershire, UK), also connected to a CR10X, logging half-hourly averages. At MOP8 soil temperature was measured at a depth of 5 cm at half-hourly intervals using a Standard Thermistor Probe and Tinytag Plus Range H datalogger (Gemini Data Loggers UK Ltd, West Sussex, UK).

In addition to the automatic soil temperature measurements, manual measurements were taken at each of the study plots whenever CO_2 exchange was measured (see section 3.1.6). This was done using a Fluke 51 digital thermometer attached to an 80PK-5A piercing probe (Fluke UK Ltd, Norfolk, UK) which was inserted to a depth of 10 cm for each measurement. For each plot the average of three measurements was recorded to account for micro-scale soil temperature heterogeneity.

Volumetric soil moisture was measured automatically throughout the study period at MOPs 2, 3, 5, 6, 7 and 8 at depths of approximately 15 cm using CS616-L Water Content Reflectometers (Campbell Scientific Ltd, Leicestershire, UK) connected to CR10X dataloggers which recorded half-hourly averages.

As with soil temperature, manual measurements of volumetric soil moisture were taken at each of the study plots whenever CO_2 exchange was measured (this was not possible in the Ridge plots due to the stony ground). Measurements were taken using a Type HH1 ThetaMeter attached to a Type ML2x ThetaProbe (Delta-T Devices Ltd, Cambridge, UK) which was inserted to a depth of 5 cm each time.

Again, the average of three measurements was recorded for each plot to account for micro-scale heterogeneity. The probe outputs, displayed in volts, were then converted to values of volumetric water content (m^3 m^{-3}) using the standard calibration for organic soils (Delta-T Devices Ltd 1999).

Air temperature (at approximately 2 m) and incident shortwave radiation were measured automatically throughout the study period at MOP4 using a HMP45AC temperature probe (Vaisala Ltd, Suffolk, UK) and a CM5 pyranometer (Kipp & Zonen Ltd, Lincolnshire, UK) respectively; each connected to a CR10x datalogger which recorded half-hourly averages. At times when the instrumentation at MOP4 failed to function, values were taken from counterpart sensors at MOPs 1 or 7.

Unfortunately, technical problems did occur with the instrumentation on a number of occasions over the two-year study period. In the case of solar radiation and air temperature this was not a problem, as there was sufficient redundancy in the instrument setup for at least one set to be functioning at all times. Unfortunately, this was not the case for the other automatically measured variables (snow depth, soil temperature and soil moisture), which were only recorded at one point for each treatment/community.

3.1.4 Plant Phenology

In both 2003 and 2004, the timing of certain conspicuous phenological events was recorded for a selection of target species in each of the experimental plots throughout the growing season. Selection of the target species was based upon the frequency of their occurrence within the study plots. Table 3-4 lists the 10, frequently occurring species that were selected for monitoring. These species are all characteristic of the Low Arctic tundra plant communities being studied; incorporating a variety of the most common deciduous and evergreen dwarf shrub and herb growth forms.

Monitoring of the phenological progress of the selected species was carried out by recording the first occurrence of each particular phenophase for each species in each plot. Phenological surveys were ideally carried out once every four days throughout the growing season. This sampling frequency was deemed to be high enough to reveal any major discrepancies between treatments/communities/years whilst still remaining practicable over the entire period of interest. Due to constraints imposed by the weather and other fieldwork demands however, it was not

always possible to maintain a four-day sampling interval in practice. In 2004, with further increases in the amount of fieldwork to be conducted, a seven-day sampling interval was the best that could be achieved; yet even this fell foul of the weather on a number of occasions. As a result, any timing differences smaller than one week are not likely to be visible in the data.

Table 3-4: Phenology survey species list.

Scientific Name	English Name	Growth Form
Andromeda polifolia	Bog Rosemary	Evergreen dwarf shrub
Arctostaphylos alpinus	Alpine Bearberry	Deciduous dwarf shrub
Betula nana	Dwarf Birch	Deciduous dwarf shrub
Diapensia lapponica	Diapensia	Evergreen cushion plant
Dryas octopetala	Mountain Avens	Evergreen dwarf shrub
Empetrum hermaphroditum	Crowberry	Evergreen dwarf shrub
Loiseleuria procumbens	Creeping Azalea	Evergreen dwarf shrub
Tofieldia pusilla	Scottish Asphodel	Perennial evergreen herb
Vaccinium uliginosum	Northern Bilberry	Deciduous dwarf shrub
Vaccinium vitis-idaea	Cowberry	Evergreen dwarf shrub

The stages of phenological development that were monitored varied from one species to another (see Table 3-5), but typically included a selection of: Leaf bud burst, completion of leaf opening, flower bud burst, flowering, flower death, fruit production, fruit ripening and leaf senescence. The stages recorded were all conspicuous enough to be observed without "excessive" observational effort, and common enough so as to occur in the majority of individuals of a given species.

Table 3-5: Phenophases monitored in each of the field study species (indicated by ×).

	Leaf Bud Burst	In Leaf	Flower Bud Burst	In Flower	Flower Death	Fruit Production	Fruit Ripe	Leaf Senescence
A. polifolia			×	×	×	×		
A. alpinus	×	×		×	×	×		×
B. nana	×	×		×				×
D. lapponica			×	×	×			
D. octopetala			×	×	×	×	×	
E. hermaphroditum					×	×	×	
L. procumbens				×	×	×		
T. pusilla			×	×	×			
V. uliginosum	×	×	×	×	×	×	×	×
V. vitis-idaea			×	×	×	×		

In 2004, the phenological observations were accompanied by fixed-point photographs of each plot. High resolution (five megapixel) images were taken using a COOLPIX 5700 digital camera (Nikon UK Ltd, Surrey, UK) mounted on a tripod at approximately 1.5 m. The tripod was always positioned in the northernmost corner of each plot. The exact leg positions of the tripod were marked with small sections of white plastic tubing so that the photographs could be taken from the exact same locations during each survey. Photographs were taken with the camera pointing straight down, each image therefore incorporating an area of about 0.25 m^2 of a plot. The photographs were analysed using a purpose written computer program (courtesy of A. J. Wiltshire) which calculated the respective red and green intensity values (R and G) of the centremost million pixels in each image, as well as a foliar phenology index (FPI), given as:

$$FPI = \frac{(G - R)}{(G + R)}$$

Equation 3-1

This index of community greenness enables a quantified comparison of the average vegetative phenology of each plot, ranging from 1.0, where everything is pure green (i.e. no red) to -1.0, where everything is red pure red (i.e. no green).

3.1.5 Plant Performance

In 2004 a series of measurements and observations was made to assess the vegetative and reproductive performance of a selection of the most abundant and frequently occurring study species.

Observations of annual stem growth increment and branching were made for *E. hermaphroditum* and *V. uliginosum*. These two species were selected for this analysis for three reasons: firstly because they occur in every study plot, secondly because both species bear annual growth scars, enabling retrospective analysis of growth/branching in previous years, and thirdly because they represent both the evergreen and the deciduous life strategies. 10 randomly selected stem samples of each species were harvested from each plot in late-August, when nearly all of that season's growth was assumed to have been completed. These samples were then transported to the laboratory at the research station where the number of new branches per year was counted and the annual growth increment was measured with digital callipers for each sample (by H. Smith). For *E. hermaphroditum* it was possible to make observations of five distinct seasons of growth and branching going back to 2000. For *V. uliginosum* it was only possible to go back four years, to 2001.

Leaf samples of *B. nana* and *V. uliginosum* were also taken during the late-August harvest. *E. hermaphroditum* was not sampled, as its small, conical leaves are not conducive to leaf area analysis. *B. nana* was included as a comparison however, as it is the only other species that occurs in all 30 plots. 50 randomly selected leaves were taken from each species per plot and transported back to the research station where they were weighed (fresh) and scanned, so that leaf area could be measured, using the computer software package, SigmaScan Pro (Version 5.0; Systat Software UK Ltd, London, UK).

Another leaf harvest had been conducted one month earlier, in late-July, in order to measure the peak season leaf nitrogen and phosphorus contents of *B. nana*, *E. hermaphroditum* and *V. uliginosum*. Enough leaves were taken for a 0.1 g (dry weight) sample of each species per plot. These leaves were transported back to the research station where they were dried for three days at 80°C and weighed. Each

0.1 g sample was then digested in a mixture of 3 ml of acid solution (97% sulphuric acid, 3% salicylic acid) and 1 ml of hydrogen peroxide (30 volumes) with a potassium sulphate and copper sulphate catalyst (15:1) at 400°C for four hours. The digested samples were then analysed for total Kjeldahl nitrogen and total phosphorus using a San Plus Segmented Flow Analyser (Skalar UK Ltd, York, UK).

In mid-July, a flower count was conducted for *A. polifolia*, *B. nana* and *V. uliginosum* within a 50×50 cm sub-quadrat of each plot. In each case the sub-quadrat was located within the northernmost corner of the plot. The three species were selected both for the frequency of their occurrence (*A. polifolia* occurs in all of the Fen plots and most of the Heath plots) and the fact that they all flower at approximately the same time, most importantly a time when it was possible to conduct a flower count. As well as counting the flowers of each of the target species within each sub-quadrat, the respective percent cover was estimated so that the number of flowers could be expressed in relation to each species' abundance.

In mid-August, a fruit count was conducted in the same sub-quadrats as the flower count. In addition to *A. polifolia*, *B. nana* and *V. uliginosum*, *E. hermaphroditum* was also included in this survey. Although *E. hermaphroditum* flowers much earlier in the season than the other three species (as soon as it is released from the snow), it bears fruit at the same time. As well as counting the fruits, five *E. hermaphroditum* berries and five *V. uliginosum* berries were harvested from each plot. It would have been preferable to harvest more, but unfortunately the sparse abundance of berries did not permit this. The samples were then transported back to the research station, where the diameter of each berry was measured with digital callipers, after which they were all dried for five days at 80°C and weighed.

3.1.6 Ecosystem Carbon Dioxide Exchange

Net ecosystem CO_2 exchange (NEE) was monitored at each of the study plots at regular intervals throughout the snow-free periods of 2003 and 2004 (see Figure 3-6).

Measurements were taken using the closed system chamber method. Clear Perspex collars, 147 mm in diameter and 90 mm high, were inserted to a depth of approximately 45 mm in each of the plots (sealed to the surface with Evo-Stik Plumbers' Mait non-setting bathroom putty (Bostik Findley Ltd, Staffordshire, UK) in the case of the Ridge community). A CPY-2 canopy exchange chamber (PP-

Figure 3-6: CO_2 exchange measurement at a Ridge plot; July, 2004.

Systems, Hertfordshire, UK) could be attached to the collars, to form a sealed column at the ecosystem-atmosphere interface. When connected to an EGM-4 infrared gas analyser (PP-Systems, Hertfordshire, UK), changes in the concentration of CO_2 within this sealed column could be measured over a set period of time, enabling calculation of the flux of CO_2 from the ecosystem to the atmosphere or *vice versa*.

In each case, measurements of NEE were taken over a period of two minutes. The chamber was then detached from the collar and flushed so as to re-equilibrate it with ambient atmospheric conditions. After flushing, the chamber was resealed to the collar and covered by an opaque plastic bucket to block out any light. After one minute (to allow for the cessation of any photosynthetic activity), CO_2 exchange was measured for a further two minutes. This second, dark measurement, with photosynthesis eliminated, equates to total ecosystem respiration (ER). Deducting this value from the non-shaded reading of NEE, in turn, enables an estimation of gross primary production (GPP).

In 2003, CO_2 flux measurements were ideally taken at all of the study plots, all within a five hour period during the middle of the day on a single day, every four days throughout the snow-free season. In practice however, equipment and weather

conditions did not always permit the realisation of the desired sampling resolution. In 2004, as with the phenology surveys, CO_2 flux measurements switched to a weekly sampling resolution.

Some modifications were made to the Perspex collars after the 2003 measurement season.

Firstly it had been observed that during the snow melt period, before the soil had thawed, water could become trapped in the collars. When temperatures dropped, the trapped water could refreeze, encasing the vegetation within the collar in a layer of ice. To alleviate this potential problem, and any others that might arise via the impediment of surface water flow, small holes were drilled in each of the collars so as to facilitate equilibration of the collar interiors with the moisture conditions of the surrounding tundra. During measurements, the holes were sealed by the rim of the chamber.

The second problem only occurred in the Heath community, where insertion of the collars resulted in considerable damage to the root systems of *E. hermaphroditum* and *B. nana*, and subsequent death of these species in and around the collar. This problem was remedied by inserting new collars, this time stuck to the surface with non-setting bathroom sealant, as in the Ridge community, rather than cut into the upper soil layer as before.

3.1.7 Statistical Analysis

Data were first tested for normality, using the Anderson-Darling test, to ascertain whether subsequent analysis should be parametric or not. If the distribution of the data was found to be significantly different from normal ($P>0.05$), the data were subsequently analysed using non-parametric tests; in all other cases, parametric tests were used.

For the plant phenology and performance data (excluding the photograph surveys and the stem growth/branching analyses), either the unpaired *t*-test or its non-parametric equivalent, the Mann-Whitney *U*-test, was used to test for significant differences between treatments within each community. Community comparisons (control data only) were made using either one-way ANOVA (analysis of variance) or its non-parametric counterpart, the Kruskal-Wallis test. For stem growth and branching, the paired *t*-test was used to compare values (corrected for natural interannual variability by dividing '+snow' values by 'controls') before and after the

start of the experiment. To avoid pseudoreplication (Hurlbert 1985), where measurements were repeated at a sub-plot scale (e.g. stem growth), analyses were only performed on the plot means. While this approach may fail to take into account potentially interesting information regarding the level of within-treatment variability, it reduces the risk of drawing erroneous conclusions from overestimation of the significance of single replicates.

The phenology index values derived from the photograph surveys were analysed using repeated measures ANOVA to test for absolute differences between treatments, as well as any interactions between survey date and treatment, which would be indicative of differences in the rate of phenological development. The same method was also used to test for differences between the communities (control data only). Similarly, the CO_2 exchange data were initially analysed using repeated measures ANOVA to test for differences between treatments and communities. Linear regression was then used to identify any proportional or absolute differences between treatments and communities that might not be revealed by repeated measures ANOVA alone. Having conducted pairwise treatment vs. treatment/community vs. community regressions, each of the respective relationships was tested for significance by ANOVA. Where the relationships were found to be significant, *t*-tests were then used to test whether the y-intercept and slope of the line of best fit differed significantly from zero and 1:1 respectively, thus indicating whether or not there were any absolute or proportional differences in the three CO_2 exchange variables (NEE, ER and GPP).

For each test, a *P*-value less than 0.05 was required for rejection of the null hypothesis that there was no difference between treatments, communities or years. The application of Bonferroni corrections was not deemed to be appropriate on mathematical, logical and practical grounds (Moran 2003). Analysis of the large, varied dataset presented in this study has required the performance of many statistical tests. Stringent application of the Bonferroni method would fail to take into account the large number of results where $P<0.05$ (although not necessarily much lower) and the extremely low probability of so many of these results occurring by chance alone. When interpreting the results of the statistical analyses it is still necessary to be aware of the fact that 5% of the conclusions are likely to be spurious. Identifying which is which however, will be down to the application of logic, rather than any statistical adjustments.

All statistical analyses were performed using the Minitab statistical software package (Release 13.20; Minitab Ltd, Coventry, UK), except for the repeated measures ANOVA, which was carried out using SPSS for Windows (Version 10.0.7; Systat Software UK Ltd, London, UK), and the regressions, which were performed using SigmaPlot 2000 (Version 6.10; Systat Software UK Ltd, London, UK).

3.2 THE MONOLITH EXPERIMENT

Having realised that it was not going to be possible to implement any treatments incorporating an accelerated snow melt at the STEPPS fieldsite, a new, complimentary, *ex situ* experiment was devised that would allow not only the effects of accelerated melting to be tested, but also those of a whole suite of snow scenarios. The new experiment employed 30 38×32×20 cm monoliths, extracted from a Heath patch at the fieldsite and transferred to 30 open-top plastic boxes of the same dimensions; 25 of which would be transported back to the gardens of the research station, the other five remaining in the field as a site control. The monolith extraction was conducted in September, 2003.

3.2.1 Site Descriptions

The five monoliths that remained at the field site were reinserted at random (in their boxes) into the same heath patch from which they had been removed. This patch was located at the northeast end of the STEPPS field site (see section 3.1.1 for a full site description).

The gardens of Abisko Scientific Research Station, where the other 25 monoliths were deployed, are situated in a large clearing in the mountain birch forest, 200 m from the banks of Lake Torneträsk (see Figure 3-1 and Figure 3-7). The gardens are flat and mostly clear of wild vegetation. For a description of the Abisko climate, see section 3.1.1.

3.2.2 Experiment Design

With the five monoliths at the fieldsite providing a site control, the 25 monoliths at the research station were randomly assigned to one of five different snow scenario treatments (five replicates per treatment):

1. Unmanipulated snow cover (control)
2. No snow cover at all (0snow)
3. Late arrival of snow cover (late)
4. Accelerated snow melt (+melt)
5. Increased snow cover (+snow)

The various treatments were implemented by deploying the monoliths to different areas of the gardens that would receive snow conditions appropriate for their respective treatments. Due to space restrictions, it was necessary to deploy monoliths of the same treatment in groups, thus introducing an element of

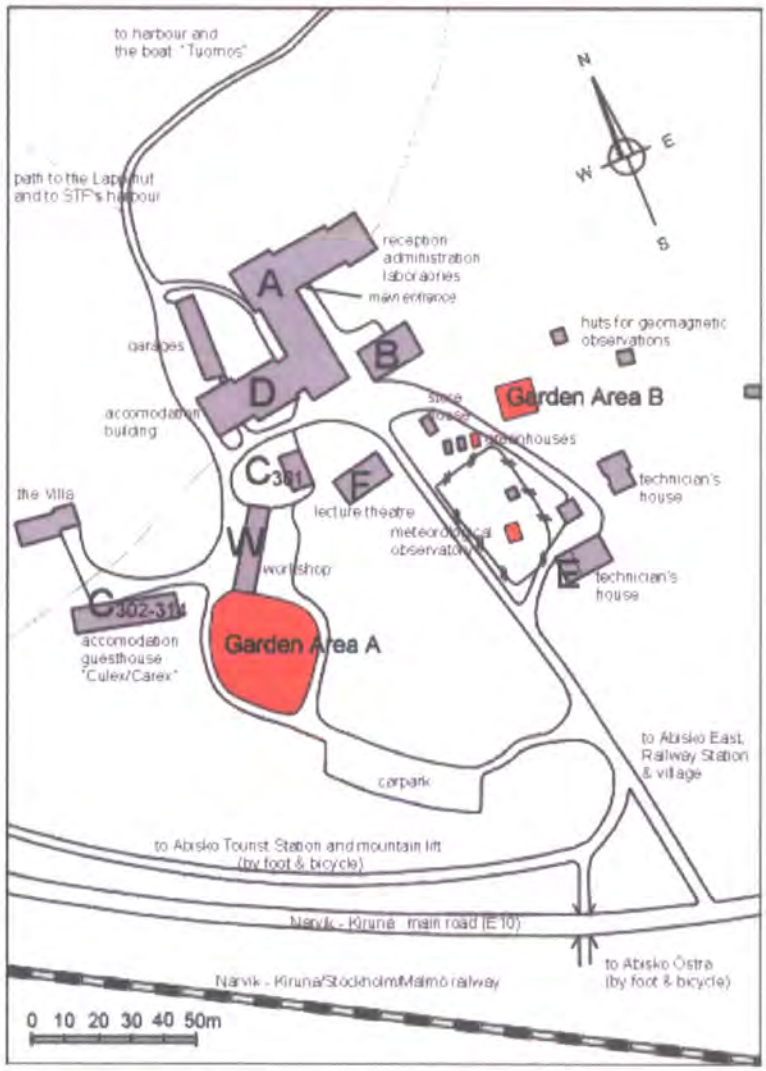

Figure 3-7: Map of Abisko Scientific Research Station showing locations of the garden areas, greenhouse and meteorological observation tower in red (Adapted from http://www.ans.kiruna.se).

Figure 3-8: The monoliths, Garden Area A; July, 2004.

pseudoreplication to the winter phase of the experiment (Hurlbert 1985). When it comes to analysing the data from this experiment, it is therefore important to bear in mind that an assumption has been made that the only factors to differ between treatments during the winter are those associated with snow cover, an assumption which may not necessarily be valid.

The 25 research station monoliths were all initially deployed in two raised sand beds in garden area A. The control and '+melt' monoliths would remain here all winter. In early November, the '+snow' monoliths were transferred to a bed in garden area B, an area where snow accumulates to greater depths and lies longer than in garden area A, due to its more sheltered location. At the same time, the 'late' and '0snow' monoliths were transferred to an outdoor greenhouse where snow could not accumulate and the internal air temperature would remain in equilibrium with that outside. In the following February, the 'late' monoliths were returned to garden area A where they could be covered with snow. At the same time, the snow that had accumulated over the '+melt' monoliths was removed with the aid of a motorised leaf-blower. These monoliths were kept free of snow for the rest of the spring. In early April, when all of the monoliths in garden area A were snow-free, the '0snow' monoliths were brought back from the greenhouse to join them. At this time, all of

the monoliths were assigned new positions within the two sand beds according to a randomised grid formation (see Figure 3-8). This was to eliminate pseudoreplication during the summer phase of the experiment. Once the '+snow' monoliths had been released from the snow in early May, they were also transferred to their new positions within the random grid.

3.2.3 Abiotic Parameters

As with the field experiment, six abiotic parameters were of particular relevance to this experiment:

1. Snow depth
2. Snow melt timing
3. Soil temperature
4. Soil moisture
5. Air temperature
6. Solar radiation

Values for these parameters were obtained automatically where possible, but otherwise were obtained by manual observation.

Snow depth and timing of snow release were measured manually for each treatment set of monoliths at regular intervals, from February until all of the monoliths were snow-free, using an aluminium snow probe.

Soil temperature was measured automatically at hourly intervals throughout the study period in one monolith per treatment at depths of approximately 5 cm using Tinytag Plus Range G dataloggers with internally mounted thermistors (Gemini Data Loggers UK Ltd, West Sussex, UK).

In addition to the automatic soil temperature measurements, manual measurements of soil temperature were taken in each monolith every time CO_2 exchange was measured (see section 3.2.7). This was done using a Fluke 51 digital thermometer attached to an 80PK-5A piercing probe which was inserted to a depth of 10 cm for each measurement.

Volumetric soil moisture was also measured in each monolith every time CO_2 exchange was measured. These measurements were taken using a Type HH1 ThetaMeter attached to a Type ML2x ThetaProbe which was inserted to a depth of

5 cm each time. As before, the probe outputs, displayed in volts, were then converted to values of volumetric water content using the standard calibration for organic soils.

Hourly average values of air temperature and incident shortwave radiation were both obtained for the period of study from the Abisko Scientific Research Station meteorological record. Both variables are measured continuously at the station's meteorological observation tower (see Figure 3-7).

3.2.4 Plant Phenology

The phenological development of *A. polifolia*, *B. nana*, *E. hermaphroditum* and *V. uliginosum* was monitored within each of the monoliths throughout the 2004 snow-free season. The four species were selected on the basis of their abundance within all of the monoliths and the fact that they were all focal species within the field experiment.

Phenological monitoring followed the same methodology employed in the field experiment (see section 3.1.4), whereby the first occurrence of each phenophase was recorded for each of the target species in each of the monoliths during surveys conducted approximately once every seven days. Table 3-6 shows the phenophases that were monitored for each of the four study species.

Table 3-6: Phenophases monitored in each of the monolith study species (indicated by ×).

	Flower Buds	Leaf Bud Burst	In Leaf	Flower Bud Burst	In Flower	Flower Death	Fruit Production	Fruit Ripe	Leaf Senescence	50% Senescence	100% Senescence
A. polifolia				×	×	×	×				
B. nana		×	×		×				×	×	×
E. hermaphroditum					×	×	×	×			
V. uliginosum	×	×	×	×	×	×			×	×	×

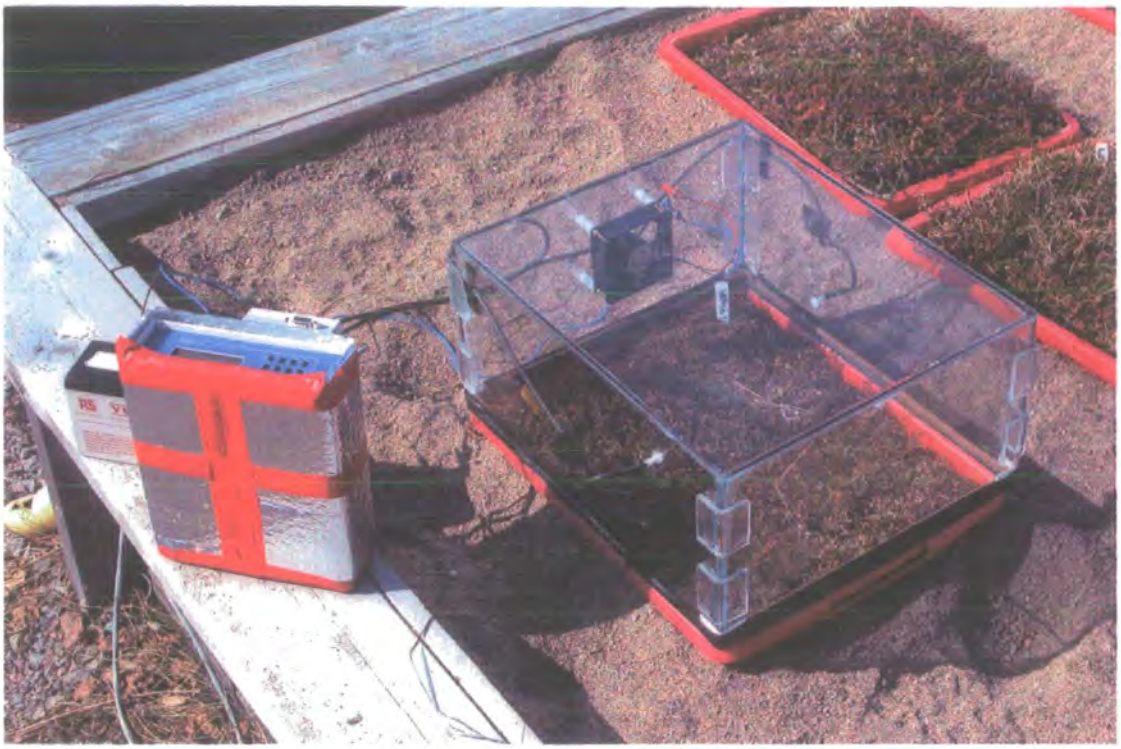

Figure 3-9: Monolith CO_2 exchange measurement; May, 2004.

3.2.5 Monolith Carbon Dioxide Exchange

NEE, ER and estimated GPP were monitored in each of the monoliths (except the site controls) approximately once every seven days throughout the 2004 snow-free season (see Figure 3-9).

The methodology was identical to that employed for the field experiment (see section 3.1.6) in all respects except that a custom built chamber was used in place of the CPY-2. The custom chamber, like the CPY-2, was made of clear Perspex and contained a small fan to promote air mixing within the chamber during measurements. No collars were required as the chamber was designed so as to fit the monolith boxes exactly (dimensions: 38×32×19 cm), forming a sealed column when placed on top. To further improve the fit and secure the seal with the monolith boxes, the rim of the chamber was lined with rubber window insulation tape.

3.2.6 Statistical Analysis

Statistical analysis of the monolith experiment data followed the same protocol as for the field experiment, with the exception that for the phenology data, either one-way ANOVA or its non-parametric counterpart was used to test for significant differences between treatments. In cases where a significant difference was

revealed, a series of *post-hoc*, pairwise, unpaired *t*-tests, or their non-parametric counterpart, were performed to identify exactly which treatments were significantly different. Again, repeated measures ANOVA and pairwise linear regressions were performed for analysis of the CO_2 exchange data.

CHAPTER 4: RESULTS OF THE FIELD EXPERIMENT

4.1 ABIOTIC PARAMETERS

4.1.1 Snow Depth

The results from the snowfence drift survey conducted in March 2003 (see Figure 4-1) give an idea of the depth and spatial extent of the snowfence drifts around the time of peak snow accumulation for that year. The areas of snow depth augmentation varied in extent from approximately 10×10 m to 20×20 m, reaching depths of up to 1.4 m at the highest points.

The plot snow depth surveys (see Figure 4-2) show further that, around the times of peak snow accumulation, snow depth was significantly greater in the '+snow' plots than the 'controls' in all three communities in both 2003 (t=5.94, -9.31, -5.12; P=0.002, <0.001, 0.001; for the Fen, Heath and Ridge communities respectively) and 2004 (W=10, 10; P=0.027, 0.026; for the Fen and Ridge; t=-16.4, P<0.001 for the Heath). The average difference in snow depth between the 'control' and '+snow' treatments for a given community in a particular year was equivalent to an increase in depth of between 200% and 1300%. In 2004, there was also a significant difference in snow depth between the 'control' plots of the three communities, with a thinner snow cover in the Ridge community than in the Fen or Heath (H=6.6, P=0.037).

Unfortunately, the records of snow depth from the automatic sensors (see Figure 4-3) are incomplete due to logger/sensor failures in both winters. Nevertheless, what data there are, are congruent with the manual snow depth surveys in terms of the depths recorded within each of the communities and the magnitude of the discrepancy between the 'control' and '+snow' treatments; although the lower values appear to have been affected by the presence of vegetation, which can interrupt the signal between the sensor and the ground/snow surface.

4.1.2 Snow Melt Timing

The timing and duration of plot snow release was, in turn, affected by the observed discrepancies in snow depth, with considerable variability observed between treatments, communities and, in some cases, years (see Figure 4-4 and Figure 4-5).

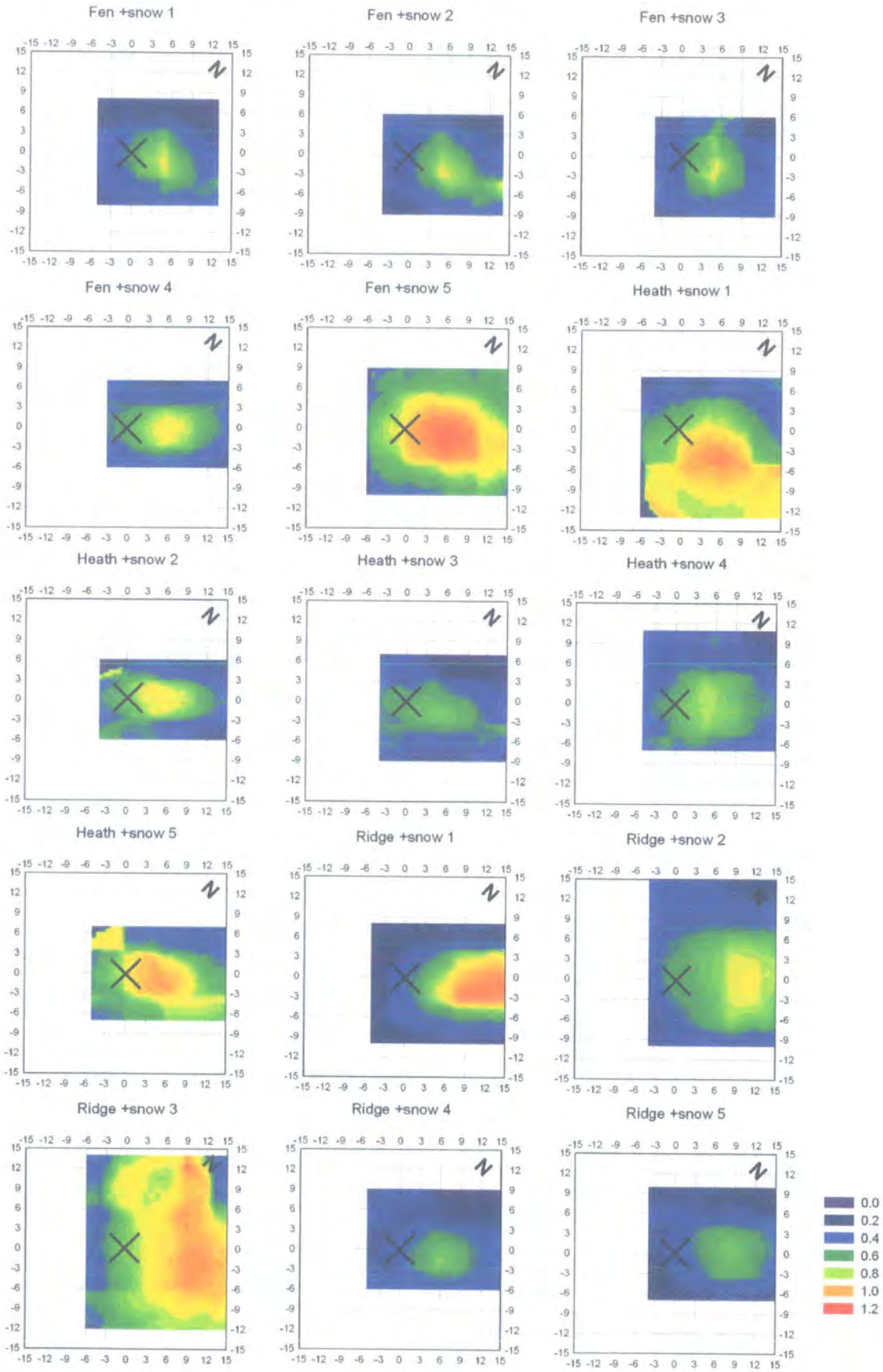

Figure 4-1: Snowfence drift snow depths and extents; March, 2003. Crosses indicate snowfence locations. Grid units and depths are in metres. Prevailing winds are from the southwest (in this case, the left).

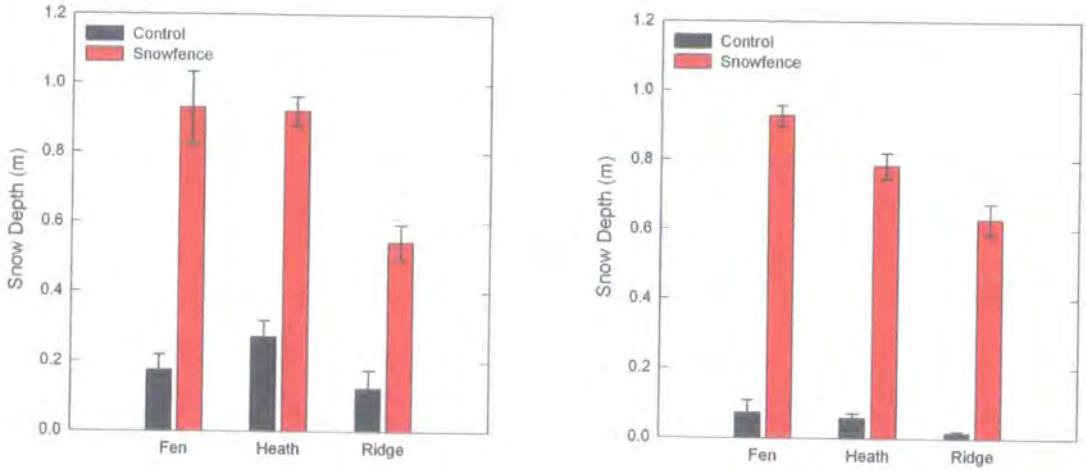

Figure 4-2: Peak snow accumulation mean study plot snow depths (± standard error; n=5) for March, 2003 (left) and 2004 (right).

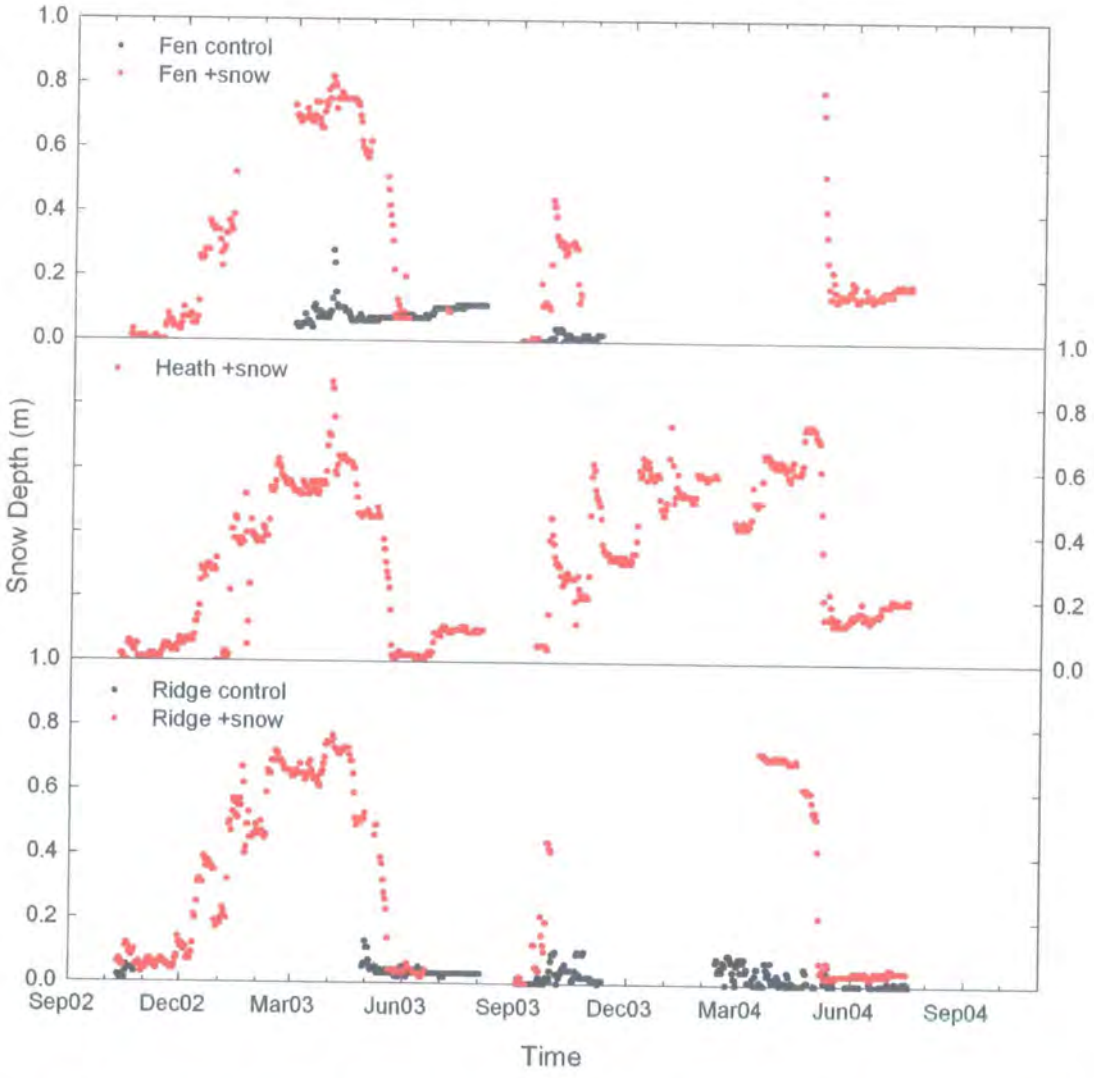

Figure 4-3: Hourly snow depth records for the two-year study period, as measured automatically at the six respective MOPs.

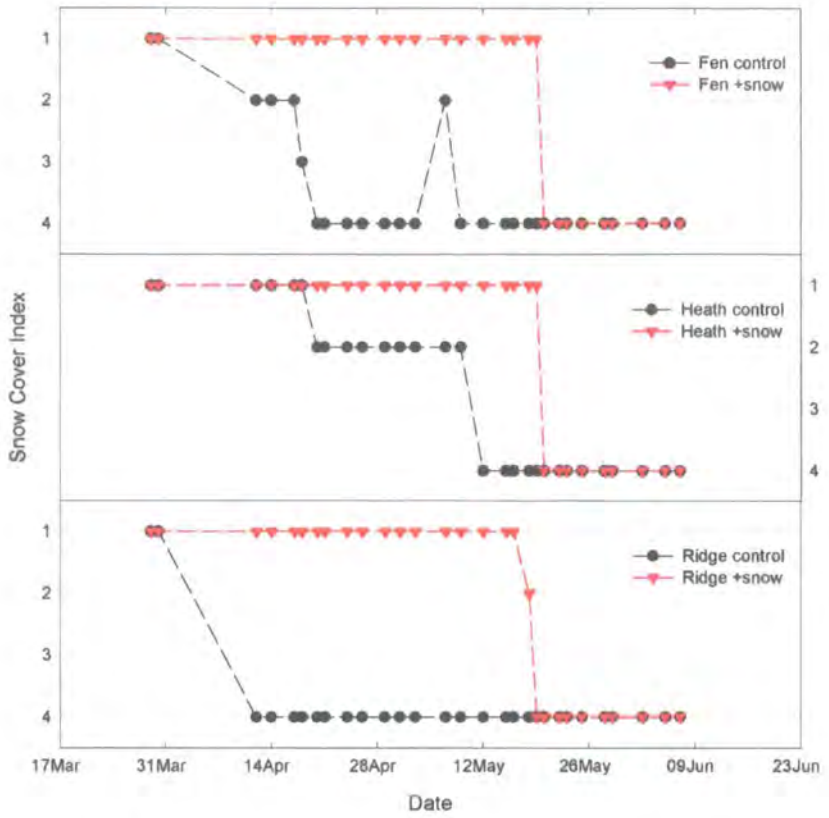

Figure 4-4: Median study plot snow cover status; spring/summer, 2003.

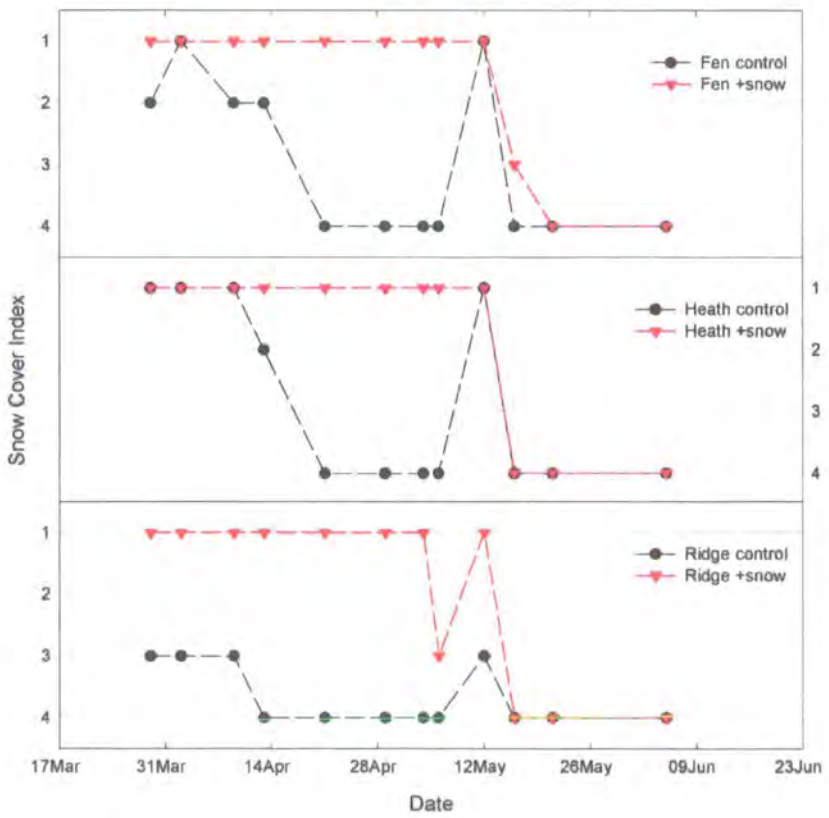

Figure 4-5: Median study plot snow cover status; spring/summer, 2004.

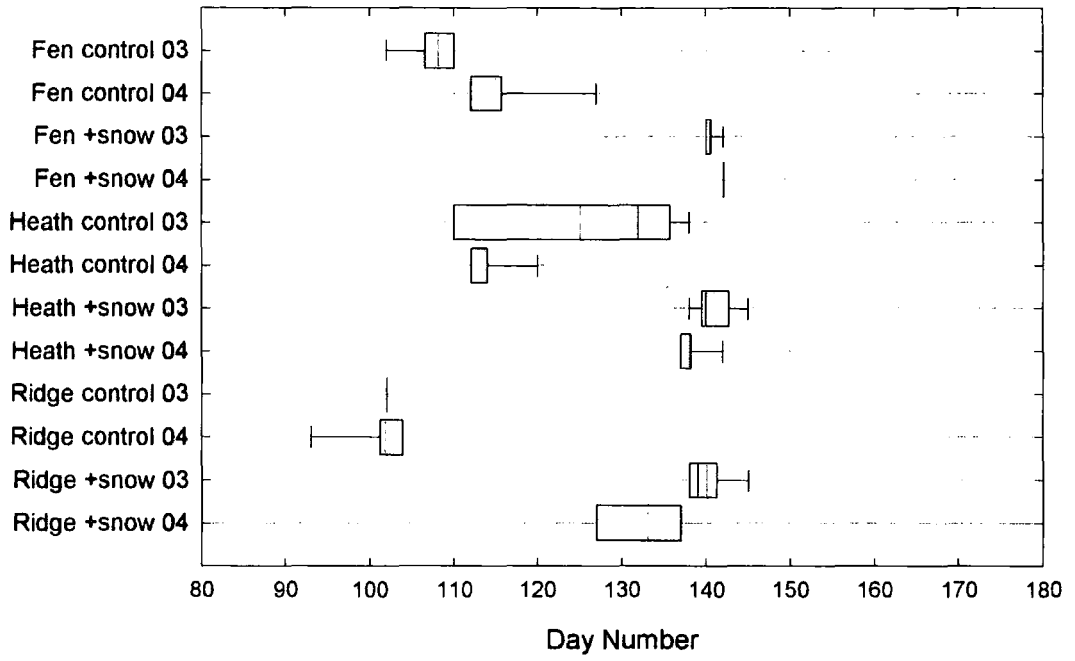

Figure 4-6: Study plot snow-free dates. The boxes and error bars display the medians, 10th, 25th, 75th, and 90th percentiles for each treatment/community/year. The red lines indicate the means (n=5).

In Figure 4-6, the results from the same snow cover status surveys are displayed in terms of the dates of the first occurrence of complete snow release (less than 10% snow cover). Although in some cases there was considerable variability between replicate plots in the same treatment/community/year (e.g. the Heath control treatment in 2003), snow release occurred significantly later in the '+snow' plots than the 'controls' in all three communities in both 2003 (W=15.0, 15.5; P=0.009, 0.015; for the Fen and Heath communities respectively; it was not possible to test the Ridge data as all of the 'control' dates are the same – earlier than the '+snow' plots) and 2004 (W=15.0, 15.0; P=0.008, 0.009; for the Heath and Ridge; it was not possible to test the Fen data as all of the '+snow' dates are the same – later than the 'controls'). The delay in snow release in the '+snow' plots ranged from approximately two to five weeks.

At this point it is important to note however that, in a number of the plots (the Ridge 'controls' in particular), in both winters, snow cover was a far more ephemeral feature than had been expected; far more ephemeral than these data alone might suggest (personal observation). In this respect, the notion of snow release date can be rather misleading, as it implies a constant winter snow cover prior to release.

Unfortunately, in the absence of sufficient winter snow cover data, there is no feasible alternative measure of snow cover duration.

4.1.3 Soil Temperature

As with snow depth, the automatic records of soil temperature (see Figure 4-7) are incomplete due to logger/sensor failures. However, it is still possible to see trends in this restricted dataset, such as the seasonal cycle from freeze to thaw and the differences between temperatures measured at the control and +snow sites in each of the communities. The biggest divergences occurred during the winter, with temperatures generally remaining warmer and more stable in areas of increased snow cover. The '+snow' soil temperatures also lagged behind the 'control' temperatures

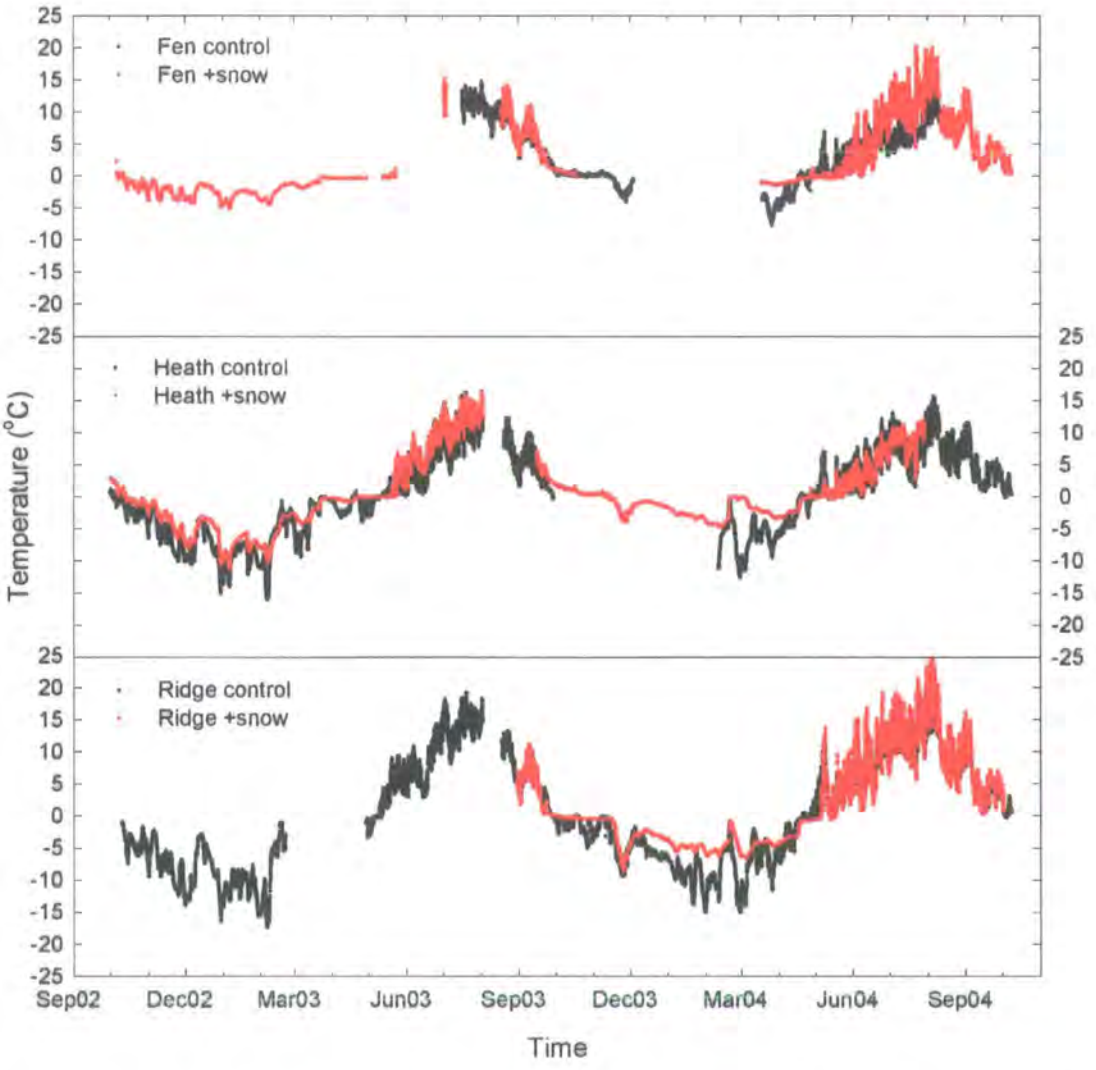

Figure 4-7: Hourly soil temperature records for the two-year study period, as measured automatically at the six respective MOPs.

during the spring thaw (in 2004 at least). There were no conspicuous differences in summer soil temperatures, except between communities (no statistical analysis was possible due to the absence of replicate measurements).

The results from the manual soil temperature surveys (see Figure 4-8) support those from the automatic measurements, revealing no significant differences between treatments in either the 2003 (t=-0.48, -0.59, -0.39; P=0.648, 0.586, 0.711; for the Fen, Heath and Ridge communities respectively) or 2004 snow-free seasons (t=-0.89, -1.25, -0.70; P=0.414, 0.252, 0.509) and showing a significant difference between communities in both years (F=144.43, 238.05; P<0.001, <0.001; for 2003 and 2004 respectively), with the warmest temperatures occurring in the Ridge plots.

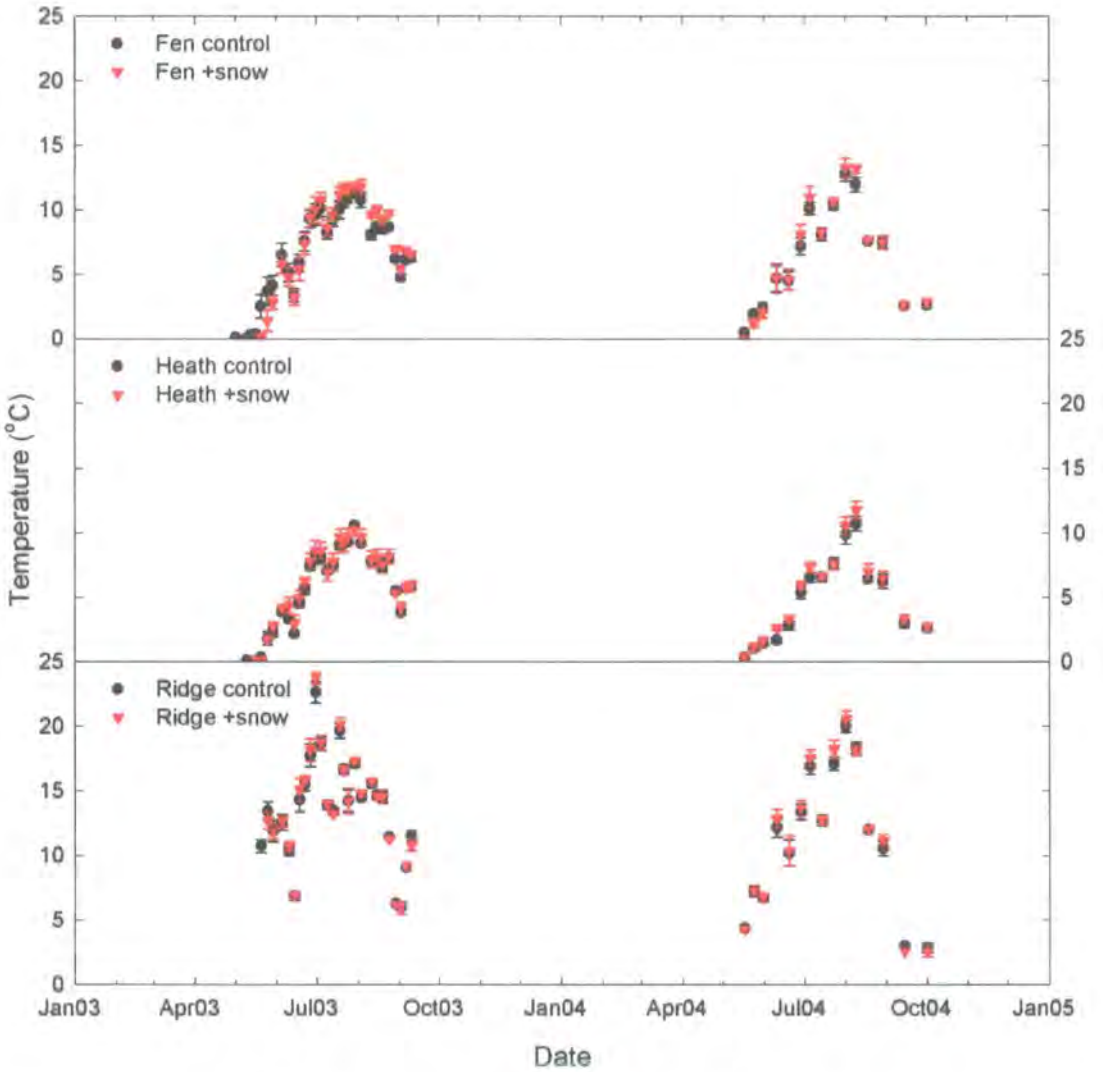

Figure 4-8: Mean study plot soil temperature (± standard error; n=5).

4.1.4 Soil Moisture

Again, problems with sensors and loggers prevented the compilation of any complete automatic soil moisture records (see Figure 4-9), but what data there are, show a clear distinction between communities, with the highest volumetric water contents occurring in the Fen and much drier conditions in the Heath and Ridge. In all three communities, rapid soil moisture fluctuations in response to rainfall events were observed during the summer months, followed by a drop to a steady low baseline value from November through until May. There does not appear to be a systematic difference between treatments (again, no statistical analysis was possible due to the absence of replicate measurements), although, similar to soil temperature, wetting-up in the spring occurred later at the '+snow' sites than at the 'controls'.

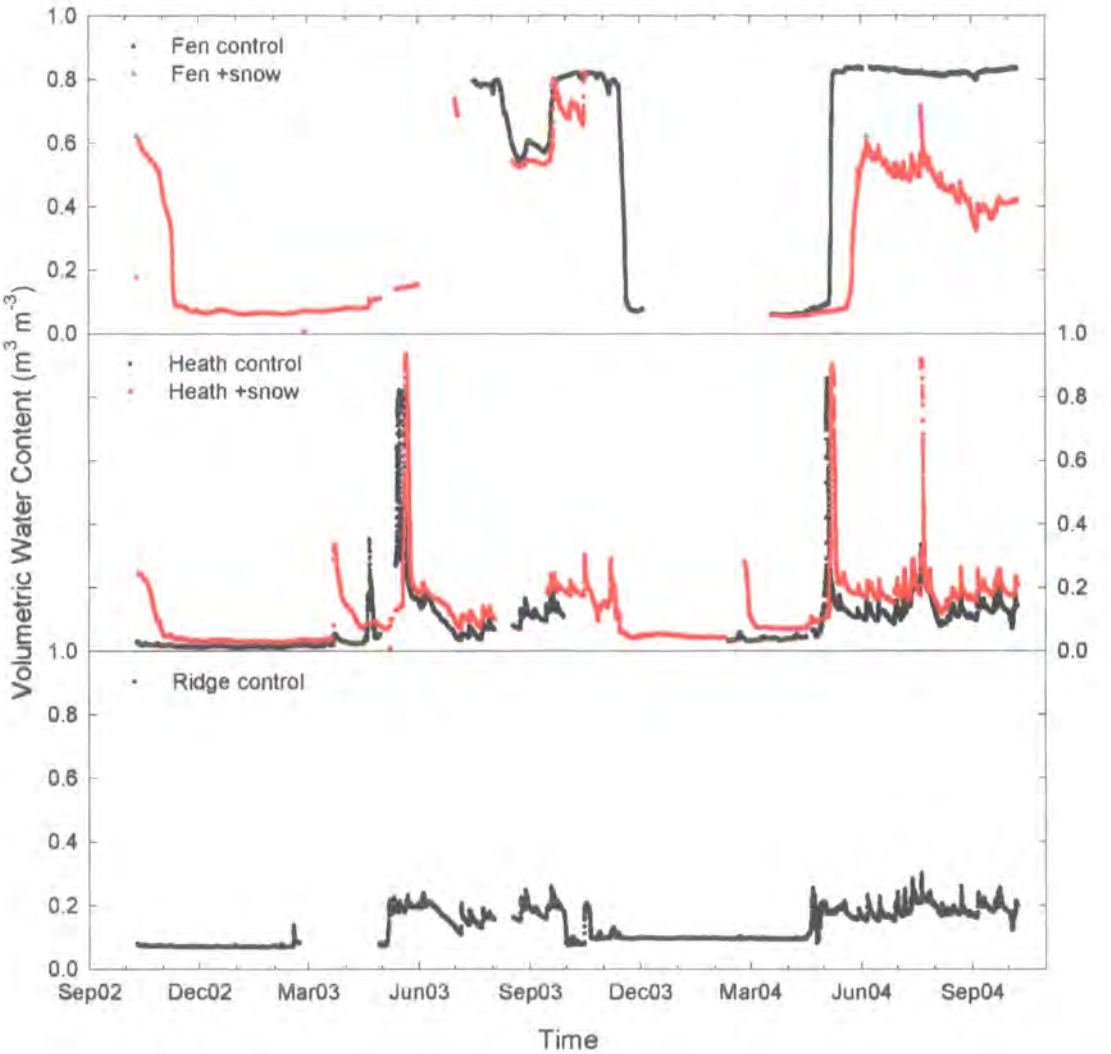

Figure 4-9: Hourly records of soil moisture for the two-year study period, as measured automatically at the five respective MOPs.

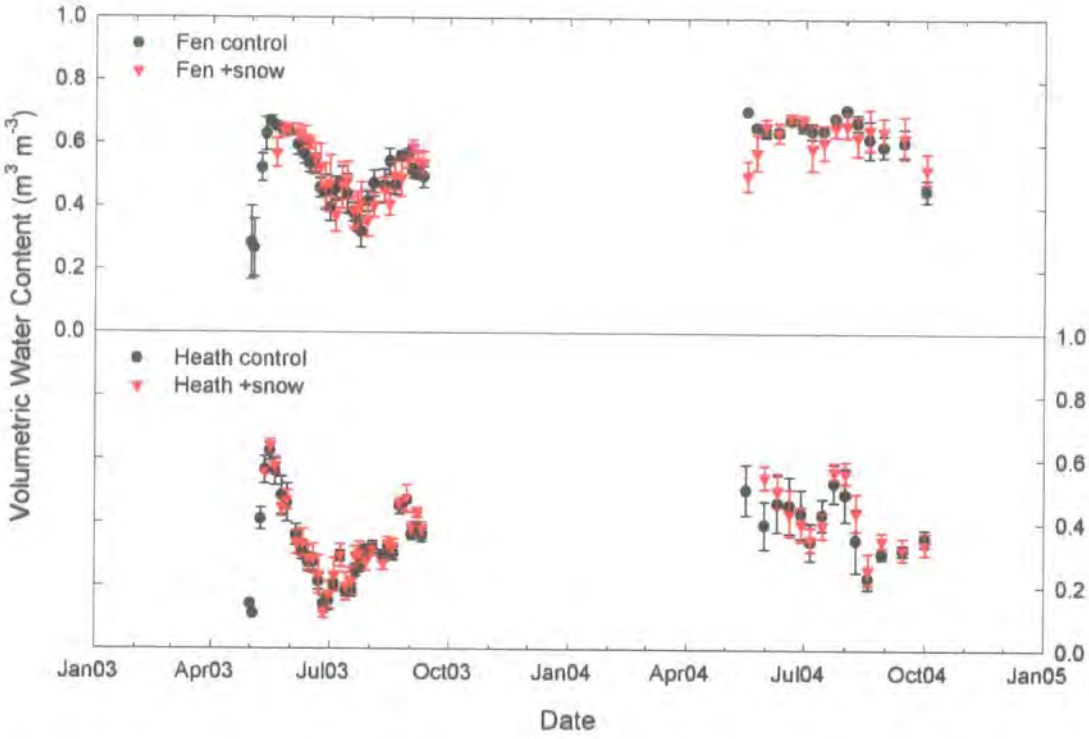

Figure 4-10: Mean study plot soil moisture (± standard error; n=5).

The results from the manual soil moisture surveys (Figure 4-10) also show a clear distinction between communities, with significantly higher volumetric water contents in the Fen community than the Heath in both snow-free seasons (t=5.35, 4.29; P=0.001, 0.008; for 2003 and 2004 respectively), but no significant difference between treatments in either 2003 (t=-0.06, -0.34; P=0.956, 0.743; for the Fen and Heath respectively) or 2004 (t=0.98, -0.47; P=0.364, 0.652).

4.1.5 Air Temperature

The fieldsite air temperature record (see Figure 4-11) exhibits a strong seasonal trend, from the freezing conditions of the winter months to temperatures in excess of 20°C in late summer as well as large, unperiodic, short-term fluctuations, especially in the winter, when the temperature was seen to rise and fall by as much as 20°C in a matter of days. On occasions in both years, such fluctuations resulted in short periods of thawing conditions in the middle of winter. It has been assumed that air temperature would have been sufficiently uniform across the site for this record to be representative of all 30 plots, but only when they were free of snow. Until snow release, the plots would be insulated from, and therefore disequilibrated with the air temperature above the snow surface. Thus, the accretion of growing degree days

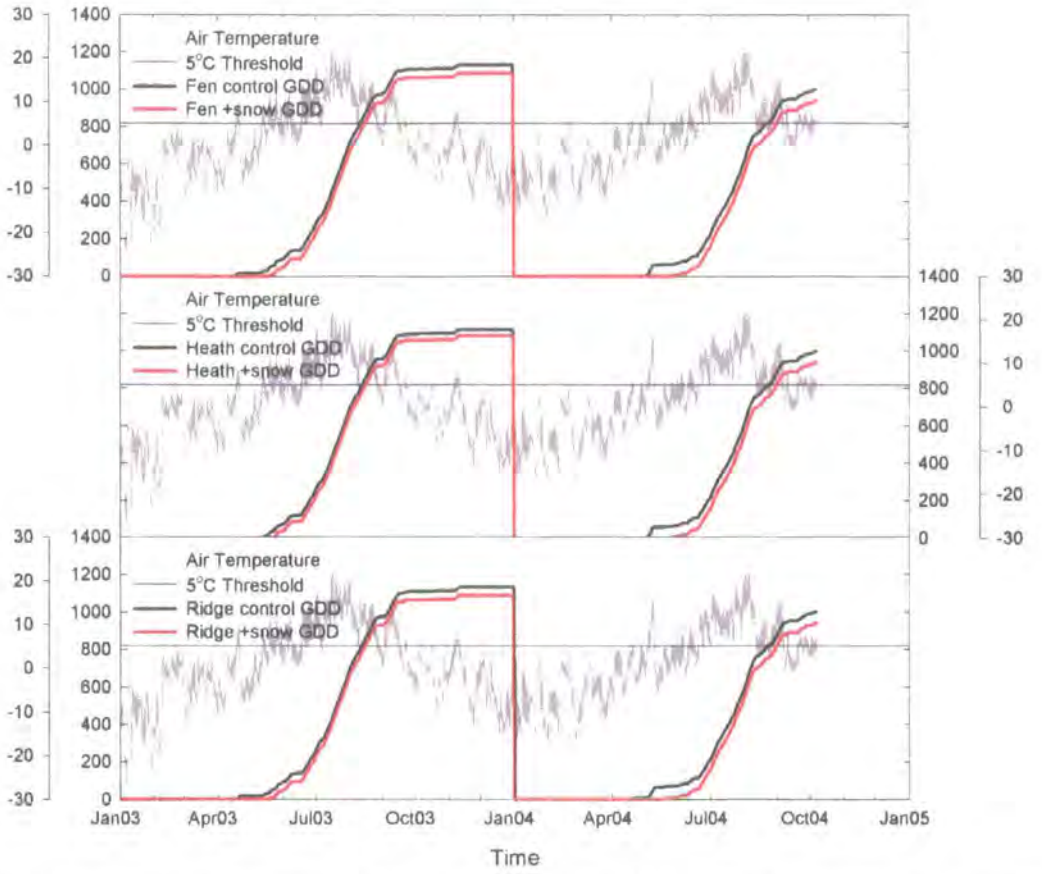

Figure 4-11: Fieldsite hourly air temperature record (°C – outer y-axis) with annual cumulative GDDs above 5°C (inner y-axis) for each treatment/community.

above 5°C (GDDs) (Molau & Mølgaard 1996) would have been affected, if only slightly, by the timing of snow release, with annual totals up to 2% lower in the '+snow plots' than the 'controls'.

4.1.6 Solar Radiation

The fieldsite record of incoming shortwave radiation (see Figure 4-12) exhibits a strong seasonal cycle, from 24 hour irradiation and peak daytime values in the region of 800 W m^{-2} in late June, to total darkness in late December. As with air temperature, it has been assumed that this record is representative of all 30 plots, with differences only occurring when plots are snow covered. Whilst snow covered, a large proportion of, if not all, incident shortwave radiation is reflected. The exact reflectivity of the snow pack is dependent on its depth and condition, but for the purpose here of estimating the annual accretion of megajoule days of shortwave radiation (MJDs) (Molau & Mølgaard 1996), the plots were assumed to be

completely shaded until they were completely snow-free. This being so, the snow release dates observed in the '+snow' plots would have resulted in annual MJD totals up to 20% lower than would have occurred in the 'controls' (Figure 4-12).

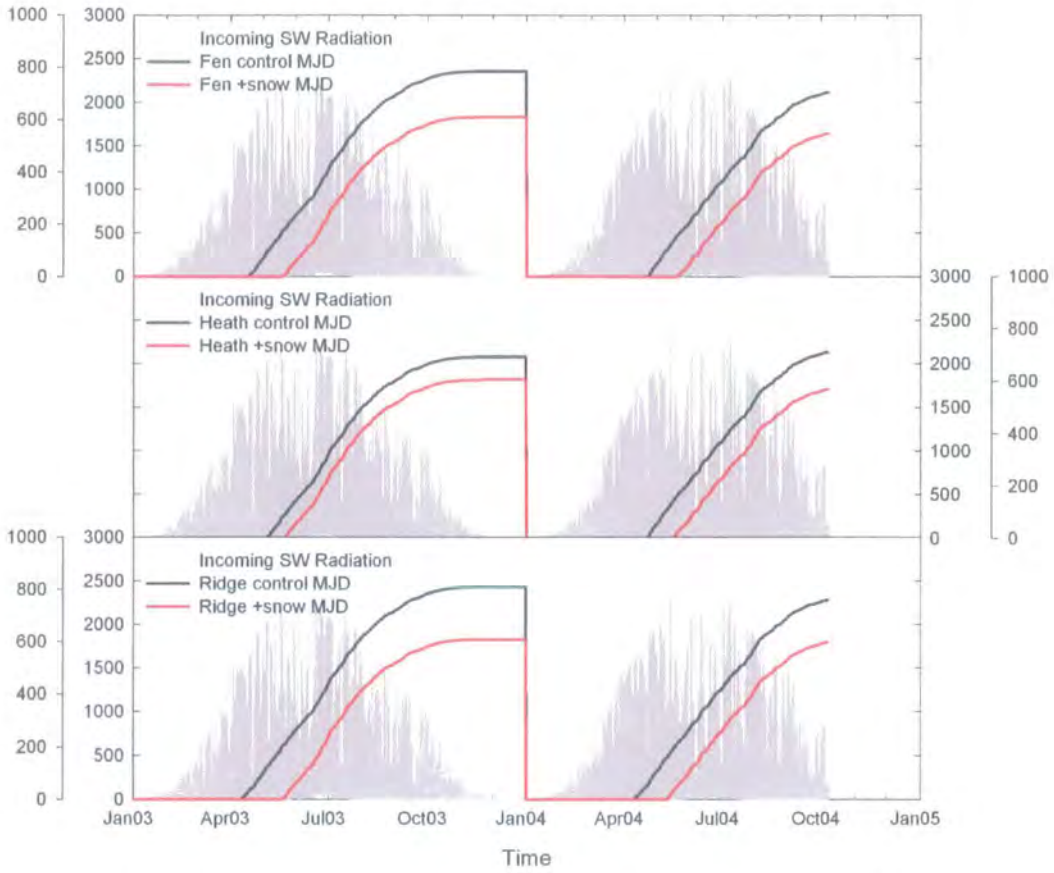

Figure 4-12: Fieldsite hourly incoming shortwave radiation record (W m^{-2} – outer y-axis) with annual cumulative MJDs (inner y-axis) for each treatment/community.

4.2 PLANT PHENOLOGY

Due to a high degree of synchronisation in the timing of phenophase occurrence within plots of the same treatment/community in a given year, in many instances there is no variance at all within the data. Where this is the case, as it is not possible to perform the relevant statistical tests, any clear differences are assumed to be significant. To indicate cases where it was not possible to perform a statistical test, a "*" is given in place of W (or H where the Kruskal-Wallis test has been used) and P values.

4.2.1 Andromeda polifolia

The dates of first occurrence of the four phenophases that were monitored for *A. polifolia* are depicted in Figure 4-13. The results of the statistical analyses of these data are displayed in Table 4-1.

The first three phenophases all occurred significantly later in the '+snow' treatments than the 'controls', with the exception of flower death in the Heath community in 2003. In the 'control' treatments, these phenophases had all occurred by the beginning of July, each occurring in the region of one to two weeks later in the '+snow' treatments, with the greatest differences occurring in 2004. The final observed phenophase, fruit production, only occurred significantly later in the Fen community in 2004, although data for the Heath community in 2003 are not available due to the infrequent occurrence of the phase in that instance.

In both years, there was a small but significant difference in the timing of flowering between communities. In each case, the phase occurred several days later in the Heath community than the Fen. The same trend was apparent for flower death, but only in 2003. The only significant differences between years, occurred with flower budburst, which was several days later in 2004 (in the Heath community only), and fruit production, which was also several days later in 2004 (in the Fen community only).

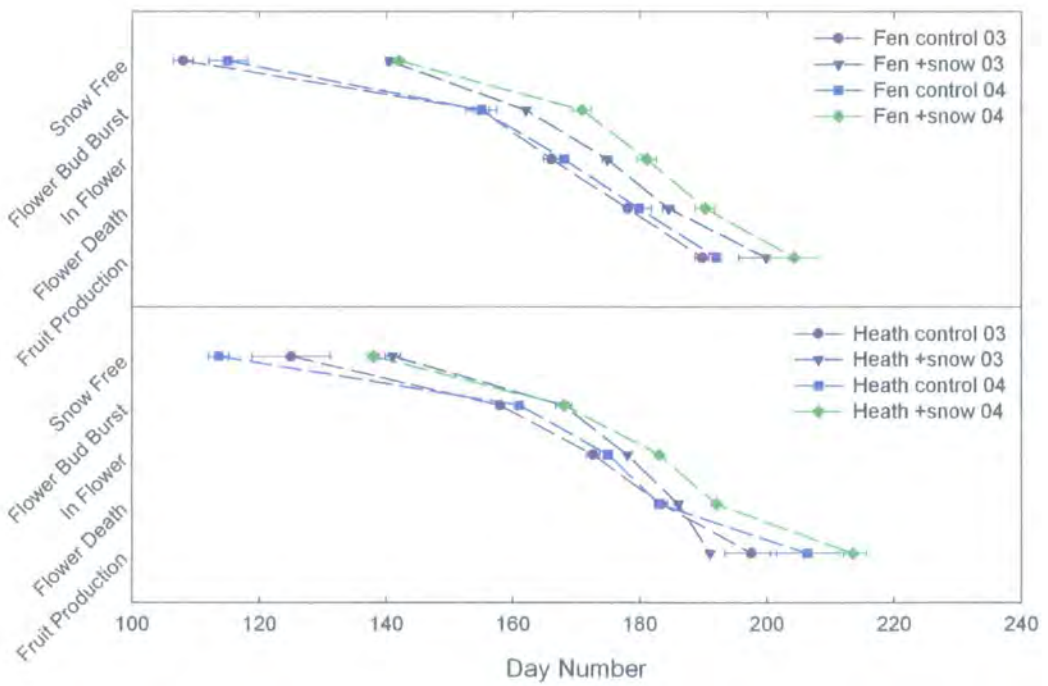

Figure 4-13: Mean dates of phenophase first occurrence for *A. polifolia* (± standard error).

Table 4-1: Results of statistical analyses of phenology data for *A. polifolia*. Where a significant result was found, a combination of '+' and '–' signs are given to indicate which of the treatments in the comparison was earlier and which was later; '0' indicates no significant difference (also shaded grey). So, for example, on the first row of this table below the headings, the '– +' indicates that flower bud burst occurred significantly later in the '+snow' treatment than in the 'control'. All subsequent phenology tables follow the same format.

Phenophase	Comparison	Difference	*W*	*P*
Flower Bud Burst	control vs. +snow (Fen 03)	– +	*	*
	control vs. +snow (Fen 04)	– +	15.0	0.001
	control vs. +snow (Heath 03)	– +	*	*
	control vs. +snow (Heath 04)	– +	*	*
	Fen vs. Heath (03)	0	*	*
	Fen vs. Heath (04)	0	*	*
	2003 vs. 2004 (Fen)	0	30.0	0.666
	2003 vs. 2004 (Heath)	– +	*	*
In Flower	control vs. +snow (Fen 03)	– +	15.0	0.009
	control vs. +snow (Fen 04)	– +	*	*
	control vs. +snow (Heath 03)	– +	*	*
	control vs. +snow (Heath 04)	– +	*	*
	Fen vs. Heath (03)	– +	15.5	0.044
	Fen vs. Heath (04)	– +	*	*
	2003 vs. 2004 (Fen)	0	*	*
	2003 vs. 2004 (Heath)	0	*	*
Flower Death	control vs. +snow (Fen 03)	– +	*	*
	control vs. +snow (Fen 04)	– +	16.5	0.019
	control vs. +snow (Heath 03)	0	*	*
	control vs. +snow (Heath 04)	– +	*	*
	Fen vs. Heath (03)	– +	*	*
	Fen vs. Heath (04)	0	*	*
	2003 vs. 2004 (Fen)	0	*	*
	2003 vs. 2004 (Heath)	0	*	*
Fruit Production	control vs. +snow (Fen 03)	0	13.0	0.081
	control vs. +snow (Fen 04)	– +	*	*
	control vs. +snow (Heath 03)			
	control vs. +snow (Heath 04)	0	8.0	0.761
	Fen vs. Heath (03)	0	11.5	0.273
	Fen vs. Heath (04)	0	*	*
	2003 vs. 2004 (Fen)	– +	*	*
	2003 vs. 2004 (Heath)	0	4.0	0.387

4.2.2 *Arctostaphylos alpinus*

The dates of first occurrence of the six phenophases that were monitored for *A. alpinus* are depicted in Figure 4-14. The results of the statistical analyses of these data are displayed in Table 4-2.

There were significant differences between treatments in *A. alpinus*' vegetative phenology, with leaf bud burst and the completion of leaf opening occurring up to three weeks later in the '+snow' treatments than the 'controls' of both communities in both years (with the exception of the Heath community in 2003), with the greatest differences occurring in 2004. In each case, both of these phenophases had occurred by the middle of June in the 'control' treatments. There was also a significant difference between treatments in the timing of leaf senescence, with later occurrence in the +snow treatment, but this was only apparent in the Fen community in 2004. No significant differences between treatments were observed at all for flowering phenology.

The only significant difference observed between communities was in the timing of leaf senescence in 2004, when it occurred nearly three weeks later in the Heath community than in the Fen (where it occurred in mid August).

In the Fen community, full leaf opening and senescence both differed

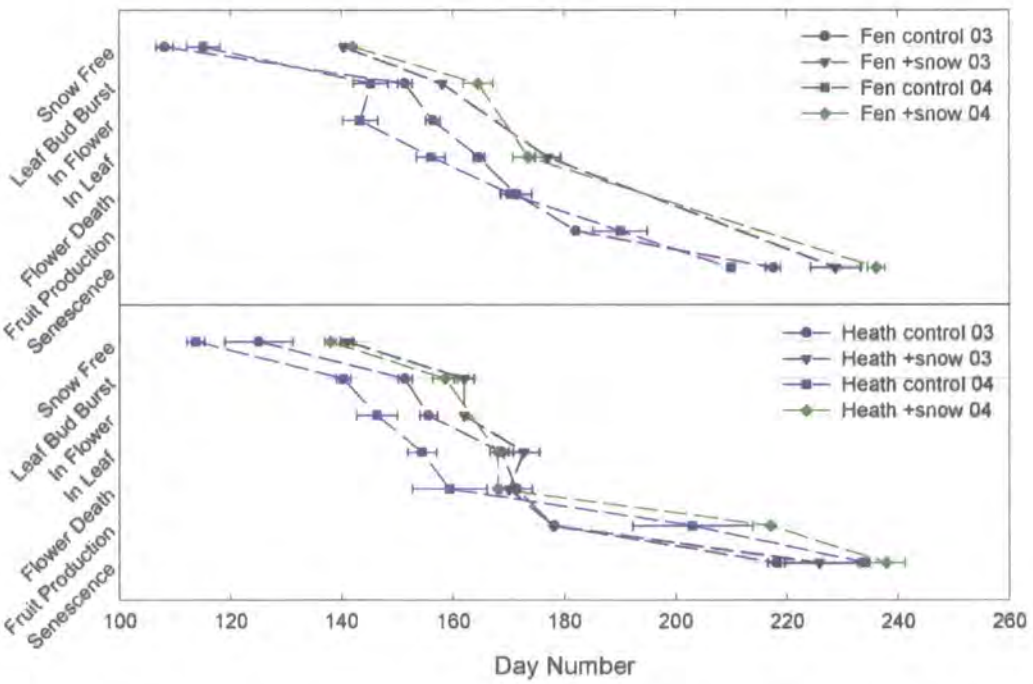

Figure 4-14: Mean dates of phenophase first occurrence for *A. alpinus* (± standard error).

significantly between years, both occurring just over a week earlier in 2003 than in 2004. The timing of leaf senescence also differed significantly between years in the Heath community, although here it occurred more than two weeks later in 2004 than in 2003.

Table 4-2: Results of statistical analyses of phenology data for *A. alpinus*.

Phenophase	Comparison	Difference	*W*	*P*
Leaf Bud Burst	**control vs. +snow (Fen 03)**	**− +**	*****	*****
	control vs. +snow (Fen 04)	**− +**	**10.0**	**0.026**
	control vs. +snow (Heath 03)	0	6.0	0.077
	control vs. +snow (Heath 04)	**− +**	**6.0**	**0.042**
	Fen vs. Heath (03)	0	10.5	1.000
	Fen vs. Heath (04)	0	18.5	0.454
	2003 vs. 2004 (Fen)	0	16.0	0.208
	2003 vs. 2004 (Heath)	0	15.0	0.072
In Flower	control vs. +snow (Fen 03)			
	control vs. +snow (Fen 04)			
	control vs. +snow (Heath 03)			
	control vs. +snow (Heath 04)			
	Fen vs. Heath (03)	0	9.5	1.000
	Fen vs. Heath (04)	0	9.5	0.814
	2003 vs. 2004 (Fen)	0	15.0	0.081
	2003 vs. 2004 (Heath)	0	9.0	0.139
In Leaf	**control vs. +snow (Fen 03)**	**− +**	**6.0**	**0.042**
	control vs. +snow (Fen 04)	**− +**	**10.0**	**0.028**
	control vs. +snow (Heath 03)	0	11.5	1.000
	control vs. +snow (Heath 04)	**− +**	*****	*****
	Fen vs. Heath (03)	0	8.0	0.302
	Fen vs. Heath (04)	0	17.0	0.838
	2003 vs. 2004 (Fen)	**+ −**	**18.0**	**0.046**
	2003 vs. 2004 (Heath)	0	15.0	0.072
Flower Death	control vs. +snow (Fen 03)			
	control vs. +snow (Fen 04)			
	control vs. +snow (Heath 03)			
	control vs. +snow (Heath 04)			
	Fen vs. Heath (03)	0	10.5	1.000
	Fen vs. Heath (04)	0	13.0	0.302
	2003 vs. 2004 (Fen)	0	11.0	1.000
	2003 vs. 2004 (Heath)	0	13.0	0.376
Fruit Production	control vs. +snow (Fen 03)			
	control vs. +snow (Fen 04)			
	control vs. +snow (Heath 03)			

	control vs. +snow (Heath 04)			
	Fen vs. Heath (03)	0	*	*
	Fen vs. Heath (04)	0	13.5	0.467
	2003 vs. 2004 (Fen)	0	*	*
	2003 vs. 2004 (Heath)	0	*	*
Senescence	control vs. +snow (Fen 03)	0	13.0	0.164
	control vs. +snow (Fen 04)	– +	*	*
	control vs. +snow (Heath 03)	0	10.5	0.693
	control vs. +snow (Heath 04)	0	*	*
	Fen vs. Heath (03)	0	15.5	1.000
	Fen vs. Heath (04)	– +	*	*
	2003 vs. 2004 (Fen)	+ –	*	*
	2003 vs. 2004 (Heath)	– +	*	*

4.2.3 Betula nana

The dates of first occurrence of the four phenophases that were monitored for *B. nana* are depicted in Figure 4-15. The results of the statistical analyses of these data are displayed in Table 4-3.

There were significant differences in vegetative phenology between treatments. The completion of leaf opening occurred significantly later in the '+snow' treatments than the 'controls' in all three communities in both years, with the exception of the Heath community in 2003. The differences were greater in 2004, with full leaf opening occurring two to three weeks later in the '+snow' treatments, than in 2003, where the differences were closer to one week. The first observed phenophase, leaf bud burst, also occurred significantly later in the '+snow' treatments in both years, although this cannot be statistically proven for the Ridge community as this phenophase always occurred before the start of the phenology surveys each spring in those plots. In the Fen and Heath communities, where sufficient data were available, the magnitude of the difference between the '+snow' and 'control' treatments also varied between years, with leaf bud burst occurring around one week later than the 'controls' in 2003, as opposed to two to three weeks later in 2004. The only significant difference between treatments in flowering phenology, was in the Ridge community in 2003 (nearly significant in 2004 also), where it occurred around one week later in the '+snow' treatment than in the 'control'.

In the 'control' treatments, leaf bud burst and opening were both completed by the beginning of May in each case. However, in 2004, full leaf opening occurred

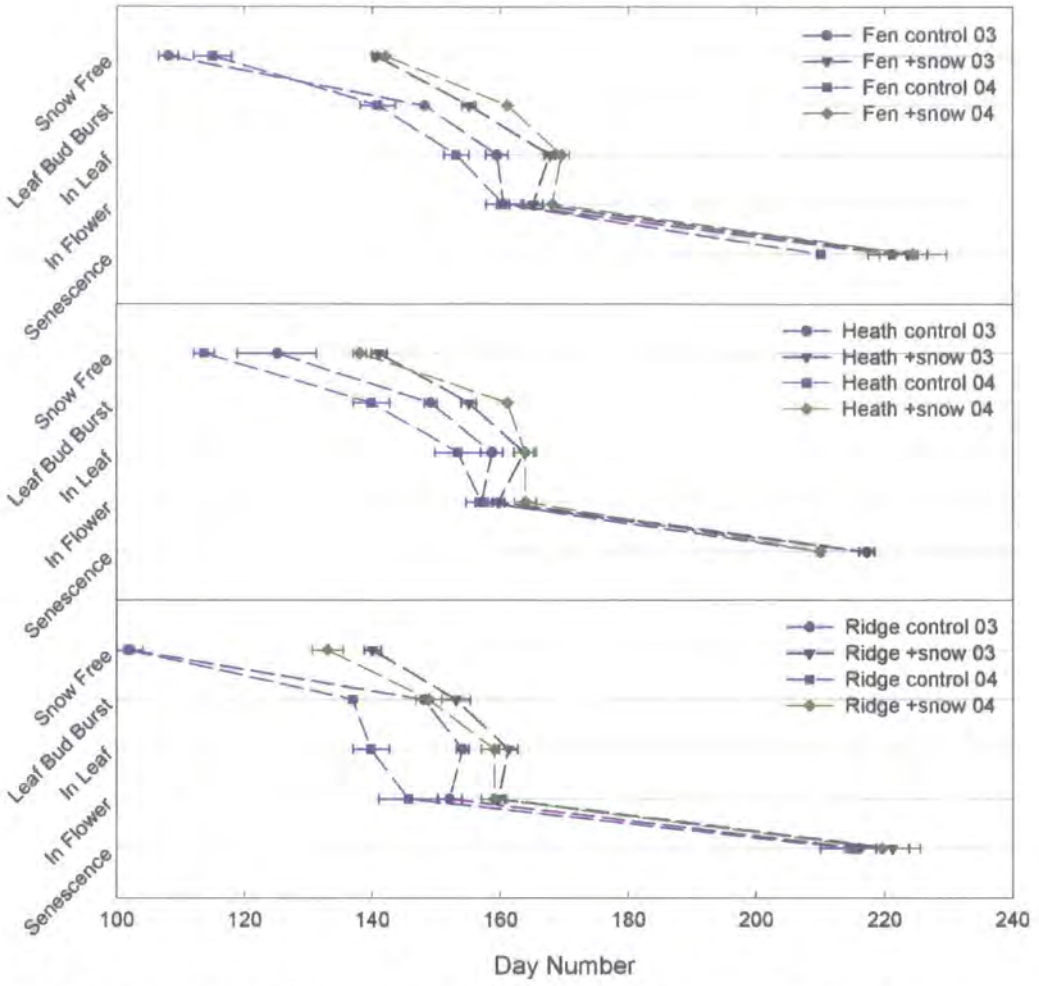

Figure 4-15: Mean dates of phenophase first occurrence for *B. nana* (± standard error).

significantly earlier in the Ridge community than in the Fen or Heath. The timing of flowering also differed significantly between communities, but only in 2003, where it occurred earlier in the Ridge community than in the Fen.

There were also significant differences between years, with both full leaf opening and senescence occurring earlier in 2004 than in 2003 in the Fen community (by around one and two weeks respectively). Full leaf opening also occurred earlier in 2004 than in 2003 in the Ridge community, whereas leaf senescence also occurred earlier in 2004 in the Heath.

Table 4-3: Results of statistical analyses of phenology data for *B. nana*.

Phenophase	Comparison	Difference	*W/H*	*P*
Leaf Bud Burst	control vs. +snow (Fen 03)	− +	*	*
	control vs. +snow (Fen 04)	− +	*	*
	control vs. +snow (Heath 03)	− +	16.5	0.019
	control vs. +snow (Heath 04)	− +	*	*
	control vs. +snow (Ridge 03)	0	*	*
	control vs. +snow (Ridge 04			
	Fen vs. Heath vs. Ridge (03)	0	1.4	0.497
	Fen vs. Heath vs. Ridge (04)	0	0.7	0.717
	2003 vs. 2004 (Fen)	0	*	*
	2003 vs. 2004 (Heath)	0	36.0	0.075
	2003 vs. 2004 (Ridge)			
In Leaf	control vs. +snow (Fen 03)	− +	15.0	0.010
	control vs. +snow (Fen 04)	− +	15.0	0.008
	control vs. +snow (Heath 03)	0	19.0	0.083
	control vs. +snow (Heath 04)	− +	18.0	0.043
	control vs. +snow (Ridge 03)	− +	16.0	0.016
	control vs. +snow (Ridge 04)	− +	15.5	0.010
	Fen vs. Heath vs. Ridge (03)	0	5.3	0.070
	Fen vs. Heath vs. Ridge (04)	+ + −	7.6	0.023
	2003 vs. 2004 (Fen)	+ −	38.0	0.029
	2003 vs. 2004 (Heath)	0	34.0	0.205
	2003 vs. 2004 (Ridge)	+ −	40.0	0.008
In Flower	control vs. +snow (Fen 03)	0	18.0	0.080
	control vs. +snow (Fen 04)			
	control vs. +snow (Heath 03)	0	21.0	0.121
	control vs. +snow (Heath 04)	0	19.5	0.075
	control vs. +snow (Ridge 03)	− +	16.5	0.022
	control vs. +snow (Ridge 04)	0	18.5	0.057
	Fen vs. Heath vs. Ridge (03)	+ 0 −	9.1	0.011
	Fen vs. Heath vs. Ridge (04)	0	5.7	0.057
	2003 vs. 2004 (Fen)	0	29.0	0.830
	2003 vs. 2004 (Heath)	0	26.0	0.661
	2003 vs. 2004 (Ridge)	0	33.0	0.292
Senescence	control vs. +snow (Fen 03)	0	23.5	0.434
	control vs. +snow (Fen 04)	0	*	*
	control vs. +snow (Heath 03)	0	27.5	1.000
	control vs. +snow (Heath 04)	0	*	*
	control vs. +snow (Ridge 03)	0	*	*
	control vs. +snow (Ridge 04)	0	25.0	0.601
	Fen vs. Heath vs. Ridge (03)	0	2.5	0.291
	Fen vs. Heath vs. Ridge (04)	0	1.8	0.407
	2003 vs. 2004 (Fen)	+ −	*	*
	2003 vs. 2004 (Heath)	+ −	*	*
	2003 vs. 2004 (Ridge)	0	*	*

4.2.4 *Diapensia lapponica*

The dates of first occurrence of the three phenophases that were monitored for *D. lapponica* are depicted in Figure 4-16. The results of the statistical analyses of these data are displayed in Table 4-4.

The data are limited for the first two phenophases as they were not seen to occur in certain plots. However, there were still some significant, if inconsistent, differences observed between treatments. Both flowering and flower death occurred later in the '+snow' treatment than the 'control' in the Ridge community, but only in 2003, with mean differences of around two weeks and a week and a half respectively. Flowering also occurred significantly later in the '+snow' treatment than the 'control' in the Heath community in 2003. Unfortunately there is insufficient data for this phenophase in the Heath community in 2004, but flower death did occur significantly later in the '+snow' treatment than the 'control' in that community in that year.

In each of the 'control' treatments, all three of the observed phenophases had occurred by the end of June in both years. No significant differences were observed in the timing of any of the phases between communities. Flower death was the only

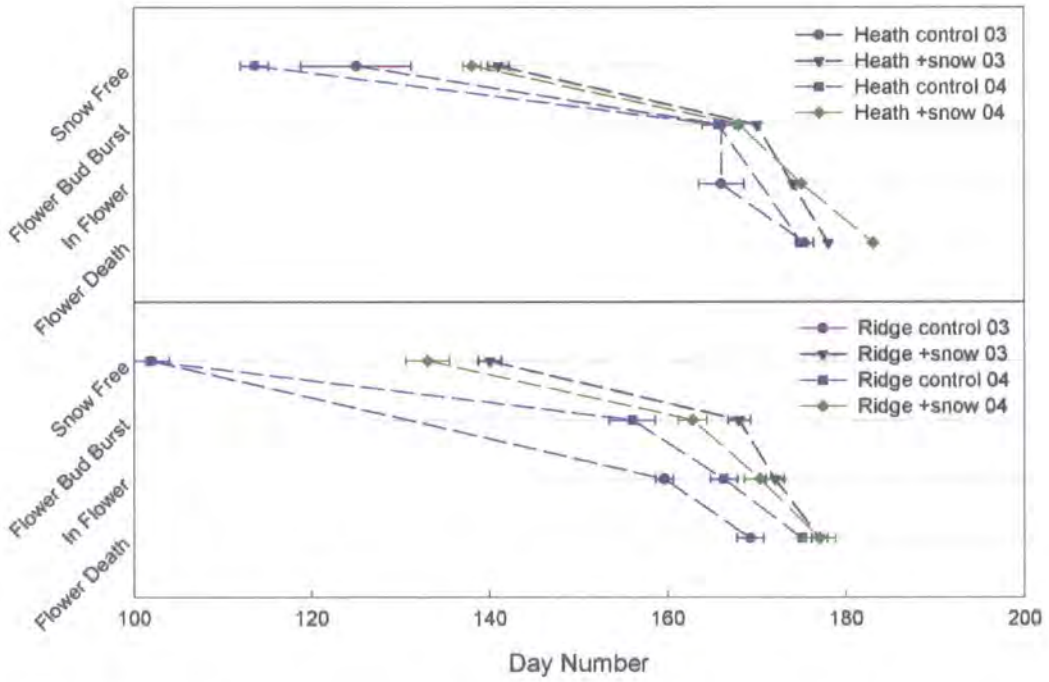

Figure 4-16: Mean dates of phenophase first occurrence for *D. lapponica* (± standard error).

phase to differ significantly between years, but only in the Ridge community; occurring around a week later in 2004 than in 2003.

Table 4-4: Results of statistical analyses of phenology data for *D. lapponica*.

Phenophase	Comparison	Difference	*W*	*P*
Flower Bud Burst	control vs. +snow (Heath 03)			
	control vs. +snow (Heath 04)	0	*	*
	control vs. +snow (Ridge 03)			
	control vs. +snow (Ridge 04)	0	13.0	0.134
	Heath vs. Ridge (03)			
	Heath vs. Ridge (04)	0	17.0	0.092
	2003 vs. 2004 (Heath)			
	2003 vs. 2004 (Ridge)			
In Flower	**control vs. +snow (Heath 03)**	**−+**	*****	*****
	control vs. +snow (Heath 04)			
	control vs. +snow (Ridge 03)	**−+**	**15.0**	**0.017**
	control vs. +snow (Ridge 04)	0	13.0	0.270
	Heath vs. Ridge (03)	0	12.0	0.143
	Heath vs. Ridge (04)			
	2003 vs. 2004 (Heath)			
	2003 vs. 2004 (Ridge)	0	17.0	0.056
Flower Death	control vs. +snow (Heath 03)	0	*	*
	control vs. +snow (Heath 04)	**−+**	*****	*****
	control vs. +snow (Ridge 03)	**−+**	**15.5**	**0.023**
	control vs. +snow (Ridge 04)	0	*	*
	Heath vs. Ridge (03)	0	20.0	0.063
	Heath vs. Ridge (04)	0	*	*
	2003 vs. 2004 (Heath)	0	*	*
	2003 vs. 2004 (Ridge)	**−+**	*****	*****

4.2.5 Dryas octopetala

The dates of first occurrence of the six phenophases that were monitored for *D. octopetala* are depicted in Figure 4-16. The results of the statistical analyses of these data are displayed in Table 4-5.

Very few significant phenological differences were observed between treatments or years for *D. octopetala*. The first observed phenophase, the appearance of conspicuous flower buds, was one exception. This phase occurred significantly later (around two weeks) in the '+snow' treatment than in the 'control', but only in 2004. This is because flower buds occurred significantly earlier in the

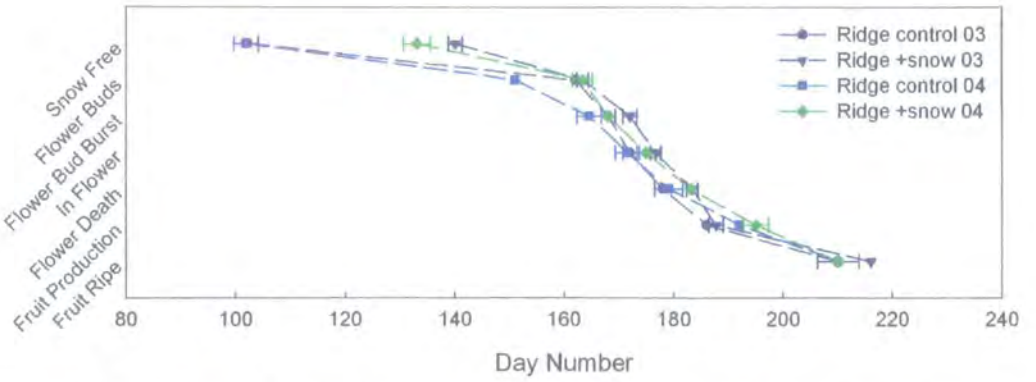

Figure 4-17: Mean dates of phenophase first occurrence for *D. octopetala* (± standard error).

'control' treatment in 2004 than in 2003. Fruit production on the other hand, occurred significantly later (several days) in 2004. The only other observed phenophase to differ significantly between treatments was flower death, which occurred several days later in the '+snow' treatment than the 'control', but only in 2003. The whole observed sequence, from the appearance of flower buds to fruit ripening, took place between the middle of June (earlier in 2004 as mentioned above) and the beginning of August each year.

Table 4-5: Results of statistical analyses of phenology data for *D. octopetala*.

Phenophase	Comparison	Difference	*W*	*P*
Flower Buds	control vs. +snow (Ridge 03)	0	*	*
	control vs. +snow (Ridge 04)	−+	*	*
	2003 vs. 2004 (Ridge)	+−	*	*
Flower Bud Burst	control vs. +snow (Ridge 03)	0	3.5	0.414
	control vs. +snow (Ridge 04)			
	2003 vs. 2004 (Ridge)	0	6.0	0.699
In Flower	control vs. +snow (Ridge 03)	0	3.5	0.224
	control vs. +snow (Ridge 04)	0	*	*
	2003 vs. 2004 (Ridge)	0	5.0	1.000
Flower Death	control vs. +snow (Ridge 03)	−+	*	*
	control vs. +snow (Ridge 04)	0	*	*
	2003 vs. 2004 (Ridge)	0	*	*
Fruit Production	control vs. +snow (Ridge 03)	0	*	*
	control vs. +snow (Ridge 04)	0	*	*
	2003 vs. 2004 (Ridge)	−+	*	*
Fruit Ripe	control vs. +snow (Ridge 03)	0	*	*
	control vs. +snow (Ridge 04)			
	2003 vs. 2004 (Ridge)			

4.2.6 *Empetrum hermaphroditum*

The dates of first occurrence of the three phenophases that were monitored for *E. hermaphroditum* are depicted in Figure 4-18. The results of the statistical analyses of these data are displayed in Table 4-6.

Flowering occurs very early in the season in *E. hermaphroditum* and quickly progresses to flower death. For this reason, flower death was the first conspicuous phenophase for which the first occurrence could be recorded in the majority of plots. In many cases, even this phenophase had already occurred prior to the start of the phenology surveys each spring (it had occurred in all of the 'control' plots by the middle of May), so data for this phase are limited. Even so, flower death is the only phase for which a significant difference between treatments was observed; in the Fen community in 2004, flower death occurred over three weeks later in the '+snow'

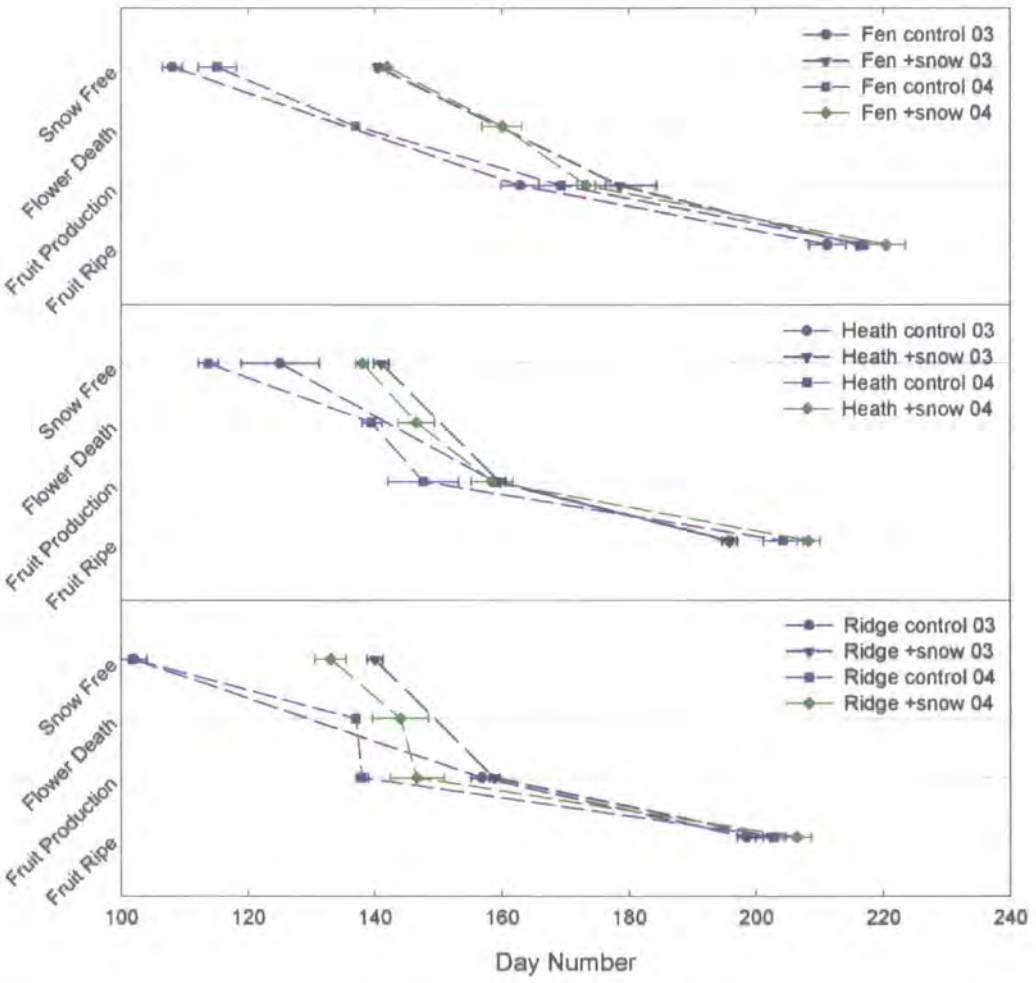

Figure 4-18: Mean dates of phenophase first occurrence for *E. hermaphroditum* (± standard error).

treatment than in the 'control'.

Though the data were insufficient to test flower death, there were significant differences between communities in both fruit production and ripening. Fruit production occurred around a month later in the Fen community than in the Ridge in 2004, while fruit ripening occurred in the region of two weeks later in the Fen community than in the Ridge or Heath in both years.

Table 4-6: Results of statistical analyses of phenology data for *E. hermaphroditum*.

Phenophase	Comparison	Difference	*W/H*	*P*
Flower Death	control vs. +snow (Fen 03)			
	control vs. +snow (Fen 04)	− +	*	*
	control vs. +snow (Heath 03)			
	control vs. +snow (Heath 04)	0	3.5	0.414
	control vs. +snow (Ridge 03)			
	control vs. +snow (Ridge 04)			
	Fen vs. Heath vs. Ridge (03)			
	Fen vs. Heath vs. Ridge (04)	0	2.5	0.287
	2003 vs. 2004 (Fen)			
	2003 vs. 2004 (Heath)			
	2003 vs. 2004 (Ridge)			
Fruit Production	control vs. +snow (Fen 03)	0	18.0	0.102
	control vs. +snow (Fen 04)	0	22.0	0.521
	control vs. +snow (Heath 03)	0	25.0	0.601
	control vs. +snow (Heath 04)	0	21.0	0.193
	control vs. +snow (Ridge 03)	0	23.5	0.407
	control vs. +snow (Ridge 04)	0	19.0	0.071
	Fen vs. Heath vs. Ridge (03)	0	3.66	0.161
	Fen vs. Heath vs. Ridge (04)	+ 0 −	**9.03**	**0.011**
	2003 vs. 2004 (Fen)	0	24.0	0.528
	2003 vs. 2004 (Heath)	0	32.0	0.386
	2003 vs. 2004 (Ridge)	+ −	**40.0**	**0.009**
Fruit Ripe	control vs. +snow (Fen 03)	0	*	*
	control vs. +snow (Fen 04)	0	*	*
	control vs. +snow (Heath 03)	0	27.5	1.000
	control vs. +snow (Heath 04)	0	22.0	0.248
	control vs. +snow (Ridge 03)	0	24.5	0.519
	control vs. +snow (Ridge 04)	0	22.5	0.270
	Fen vs. Heath vs. Ridge (03)	+ − −	**10.9**	**0.004**
	Fen vs. Heath vs. Ridge (04)	+ − −	**9.7**	**0.008**
	2003 vs. 2004 (Fen)	0	*	*
	2003 vs. 2004 (Heath)	− +	**15.0**	**0.008**
	2003 vs. 2004 (Ridge)	0	19.0	0.075

Both fruit production and ripening also differed significantly between years in certain cases. Fruit production occurred around three weeks earlier in 2004 than in 2003 in the Ridge community, whereas fruit ripening occurred around a week later in 2004 than in 2003 in the Heath.

4.2.7 Loiseleuria procumbens

The dates of first occurrence of the three phenophases that were monitored for *L. procumbens* are depicted in Figure 4-19. The results of the statistical analyses of these data are displayed in Table 4-7.

No significant differences between treatments or years were found for any of the observed phenophases. However, a very nearly significant difference between treatments was observed for flowering in 2003, where it occurred around two weeks later in the '+snow' treatment than the 'control'. No differences were observed whatsoever for flower death or fruit production, which in each case, occurred in late June and early July respectively.

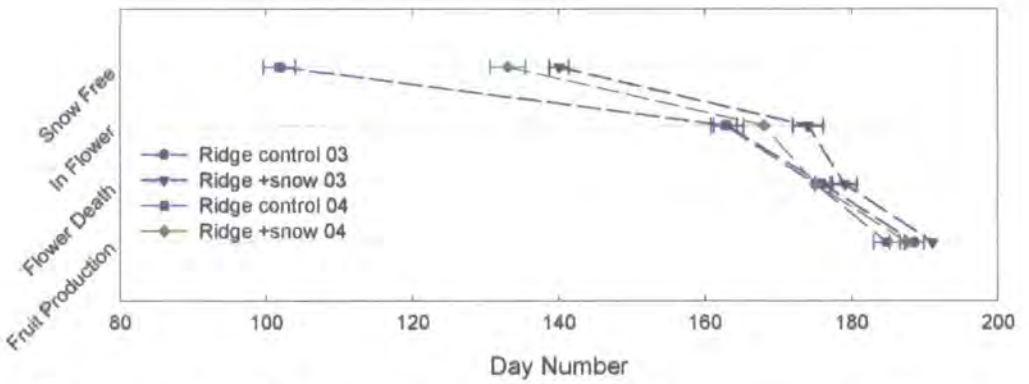

Figure 4-19: Mean dates of phenophase first occurrence for *L. procumbens* (± standard error).

Table 4-7: Results of statistical analyses of phenology data for *L. procumbens*.

Phenophase	Comparison	Difference	*W*	*P*
In Flower	control vs. +snow (Ridge 03)	0	11.0	0.052
	control vs. +snow (Ridge 04)	0	*	*
	2003 vs. 2004 (Ridge)	0	20.0	0.655
Flower Death	control vs. +snow (Ridge 03)	0	14.0	0.285
	control vs. +snow (Ridge 04)	0	*	*
	2003 vs. 2004 (Ridge)	0	*	*
Fruit Production	control vs. +snow (Ridge 03)	0	*	*
	control vs. +snow (Ridge 04)	0	22.0	0.456
	2003 vs. 2004 (Ridge)	0	26.0	0.156

4.2.8 Tofieldia pusilla

The dates of first occurrence of the three phenophases that were monitored for *T. pusilla* are depicted in Figure 4-20. The results of the statistical analyses of these data are displayed in Table 4-8.

Although no significant differences between treatments were observed for the appearance of conspicuous flower buds, flowering was found to occur significantly later (around one week) in the '+snow' treatment than in the 'control' in both years. The only significant difference associated with flower death was between years; it occurred sever days later in 2004 than in 2003. Overall, the phenology observed for *T. pusilla* was generally later than that described for any of the previous species, with the entire observed phenological sequence occurring between late June and the middle of July each year.

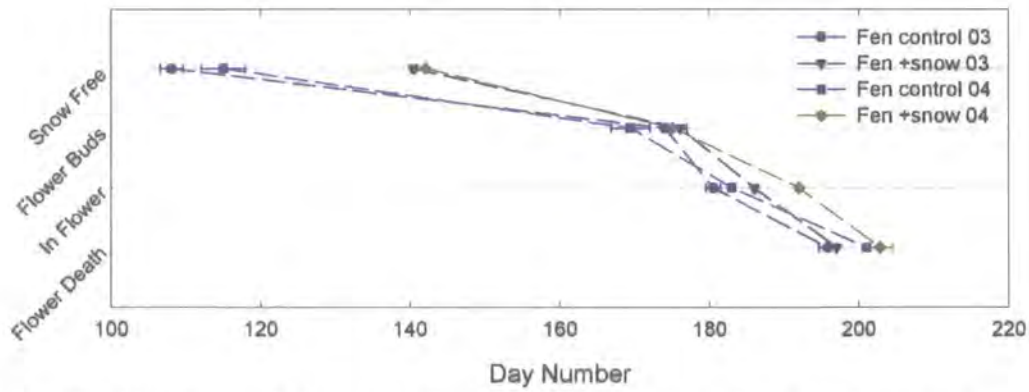

Figure 4-20: Mean dates of phenophase first occurrence for *T. pusilla* (± standard error).

Table 4-8: Results of statistical analyses of phenology data for *T. pusilla*.

Phenophase	Comparison	Difference	*W*	*P*
Flower Buds	control vs. +snow (Fen 03)	0	*	*
	control vs. +snow (Fen 04)	0	*	*
	2003 vs. 2004 (Fen)	0	*	*
In Flower	control vs. +snow (Fen 03)	– +	*	*
	control vs. +snow (Fen 04)	– +	*	*
	2003 vs. 2004 (Fen)	0	*	*
Flower Death	control vs. +snow (Fen 03)	0	*	*
	control vs. +snow (Fen 04)	0	*	*
	2003 vs. 2004 (Fen)	– +	*	*

4.2.9 Vaccinium uliginosum

The dates of first occurrence of the eight phenophases that were monitored for *V. uliginosum* are depicted in Figure 4-21. The results of the statistical analyses of these data are displayed in Table 4-9.

The eight phenophases observed in *V. uliginosum* span a large proportion of the snow-free season, from the first occurrences of leaf bud burst in the middle of May to leaf senescence in mid August. The timing of occurrence of the first three observed phenophases differed significantly between treatments in all communities in both years, with the exception of the Heath community in 2003 and, in the case of leaf bud burst, the Fen community in 2004. In each instance, these phenophases occurred later in the '+snow' treatments than in the 'controls', with differences ranging from one to three weeks, the greatest differences occurring in 2004. Fewer significant differences between treatments were observed with the later phenophases. As with the earlier phases, flowering occurred significantly later in the '+snow' treatments than in the 'controls', but only in the Heath and Ridge communities, and only in 2004. Flower death similarly occurred later in the '+snow' treatment than the 'control', but only in the Ridge community. The timing of the final phenophases, fruit production, leaf senescence and fruit ripening, was not found to differ significantly between treatments.

Although rather inconsistent, there were a number of significant phenological differences between communities. In 2003, the completion of leaf opening occurred around a week later in the Heath community than in the Ridge, as did flower death.

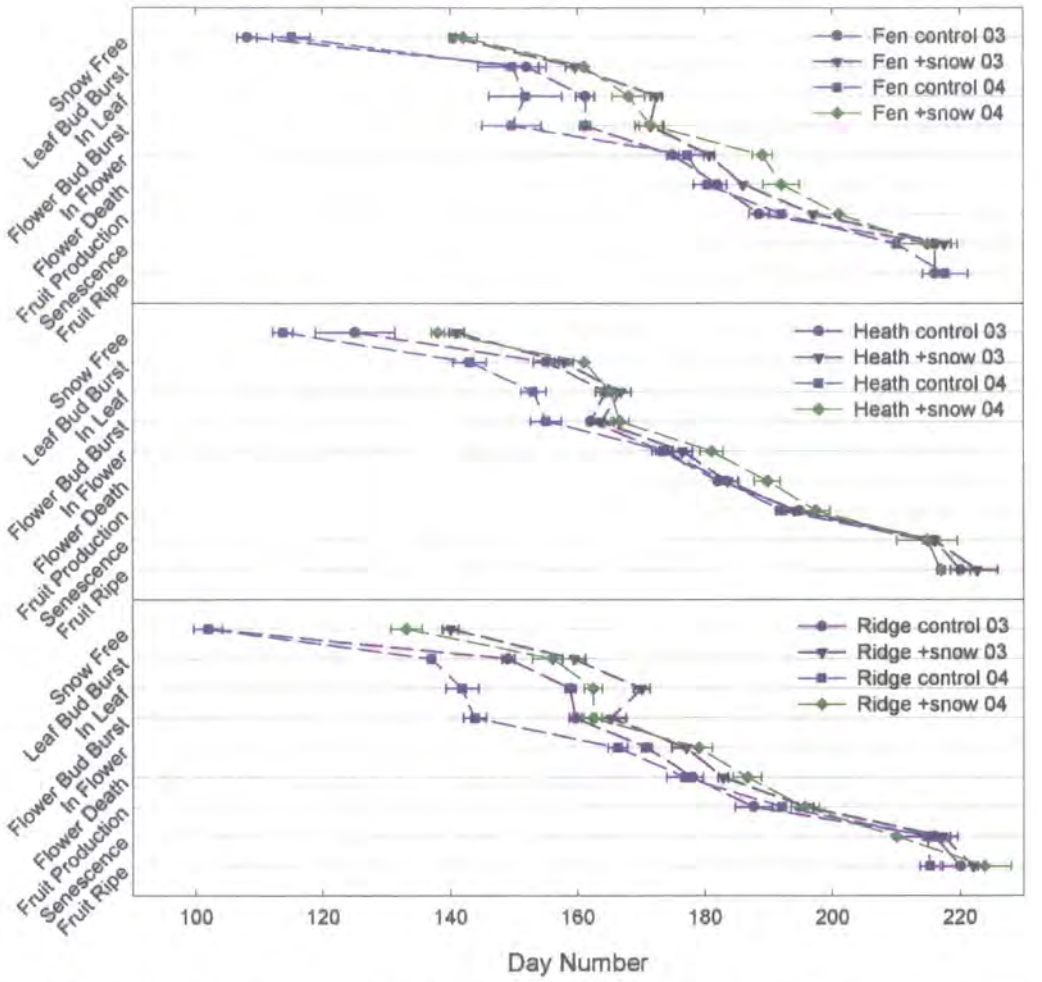

Figure 4-21: Mean dates of phenophase first occurrence for *V. uliginosum* (± standard error).

In 2004 on the other hand, it was flowering that occurred around a week later in the Heath community than in the Ridge.

In the Ridge community, the first four phenophases all occurred significantly earlier (around two weeks, three weeks, three weeks and several days respectively) in 2004 than in 2003. Similarly, in the Heath community, the first two phenophases occurred around two weeks earlier in 2004 than in 2003. In the Fen community, the only significant differences between years were found with flower bud burst and leaf senescence, both occurring earlier in 2004 than in 2003.

Table 4-9: Results of statistical analyses of phenology data for *V. uliginosum*.

Phenophase	Comparison	Difference	*W/H*	*P*
Leaf Bud Burst	control vs. +snow (Fen 03)	– +	17.0	0.025
	control vs. +snow (Fen 04)	0	*	*
	control vs. +snow (Heath 03)	0	23.0	0.345
	control vs. +snow (Heath 04)	– +	*	*
	control vs. +snow (Ridge 03)	– +	15.5	0.012
	control vs. +snow (Ridge 04)	– +	*	*
	Fen vs. Heath vs. Ridge (03)	0	4.7	0.095
	Fen vs. Heath vs. Ridge (04)	0	2.7	0.262
	2003 vs. 2004 (Fen)	0	23.0	1.000
	2003 vs. 2004 (Heath)	+ –	34.0	0.033
	2003 vs. 2004 (Ridge)	+ –	*	*
In Leaf	control vs. +snow (Fen 03)	– +	15.0	0.010
	control vs. +snow (Fen 04)	– +	*	*
	control vs. +snow (Heath 03)	0	22.5	0.319
	control vs. +snow (Heath 04)	– +	16.0	0.015
	control vs. +snow (Ridge 03)	– +	15.0	0.009
	control vs. +snow (Ridge 04)	– +	15.0	0.009
	Fen vs. Heath vs. Ridge (03)	0 + –	6.4	0.040
	Fen vs. Heath vs. Ridge (04)	0	4.7	0.097
	2003 vs. 2004 (Fen)	0	33.0	0.293
	2003 vs. 2004 (Heath)	+ –	40.0	0.009
	2003 vs. 2004 (Ridge)	+ –	40.0	0.009
Flower Bud Burst	control vs. +snow (Fen 03)	– +	15.0	0.026
	control vs. +snow (Fen 04)	– +	15.0	0.017
	control vs. +snow (Heath 03)	0	*	*
	control vs. +snow (Heath 04)	– +	16.0	0.015
	control vs. +snow (Ridge 03)	– +	18.0	0.042
	control vs. +snow (Ridge 04)	– +	15.0	0.008
	Fen vs. Heath vs. Ridge (03)	0	4.5	0.108
	Fen vs. Heath vs. Ridge (04)	0	5.2	0.073
	2003 vs. 2004 (Fen)	+ –	38.0	0.029
	2003 vs. 2004 (Heath)	0	*	*
	2003 vs. 2004 (Ridge)	+ –	40.0	0.009
In Flower	control vs. +snow (Fen 03)	0	10.5	0.061
	control vs. +snow (Fen 04)	0	11.0	0.096
	control vs. +snow (Heath 03)	0	21.0	0.174
	control vs. +snow (Heath 04)	– +	17.0	0.040
	control vs. +snow (Ridge 03)	0	18.0	0.080
	control vs. +snow (Ridge 04)	– +	10.0	0.025
	Fen vs. Heath vs. Ridge (03)	0	5.2	0.076
	Fen vs. Heath vs. Ridge (04)	0 + –	6.4	0.041
	2003 vs. 2004 (Fen)	0	15.0	0.457
	2003 vs. 2004 (Heath)	0	24.0	0.515
	2003 vs. 2004 (Ridge)	+ –	35.0	0.013

Flower Death	control vs. +snow (Fen 03)	0	*	*
	control vs. +snow (Fen 04)			
	control vs. +snow (Heath 03)	0	*	*
	control vs. +snow (Heath 04)	0	*	*
	control vs. +snow (Ridge 03)	**– +**	*	*
	control vs. +snow (Ridge 04)	**– +**	**18.0**	**0.043**
	Fen vs. Heath vs. Ridge (03)	**0 + –**	**8.2**	**0.017**
	Fen vs. Heath vs. Ridge (04)	0	2.8	0.251
	2003 vs. 2004 (Fen)	0	16.0	1.000
	2003 vs. 2004 (Heath)	0	*	*
	2003 vs. 2004 (Ridge)	0	*	*
Fruit Production	control vs. +snow (Fen 03)			
	control vs. +snow (Fen 04)			
	control vs. +snow (Heath 03)	0	28.0	1.000
	control vs. +snow (Heath 04)	0	*	*
	control vs. +snow (Ridge 03)	0	18.5	0.057
	control vs. +snow (Ridge 04)	0	*	*
	Fen vs. Heath vs. Ridge (03)	0	3.9	0.144
	Fen vs. Heath vs. Ridge (04)	0	0.0	1.000
	2003 vs. 2004 (Fen)	0	*	*
	2003 vs. 2004 (Heath)	0	*	*
	2003 vs. 2004 (Ridge)	0	*	*
Senescence	control vs. +snow (Fen 03)	0	*	*
	control vs. +snow (Fen 04)	0	*	*
	control vs. +snow (Heath 03)	0	*	*
	control vs. +snow (Heath 04)	0	27.5	1.000
	control vs. +snow (Ridge 03)	0	*	*
	control vs. +snow (Ridge 04)	0	*	*
	Fen vs. Heath vs. Ridge (03)	0	0	1
	Fen vs. Heath vs. Ridge (04)	0	1.1	0.584
	2003 vs. 2004 (Fen)	**+ –**	*	*
	2003 vs. 2004 (Heath)	0	*	*
	2003 vs. 2004 (Ridge)	0	*	*
Fruit Ripe	control vs. +snow (Fen 03)			
	control vs. +snow (Fen 04)			
	control vs. +snow (Heath 03)	0	9.5	0.814
	control vs. +snow (Heath 04)	0	*	*
	control vs. +snow (Ridge 03)	0	*	*
	control vs. +snow (Ridge 04)	0	14.5	0.143
	Fen vs. Heath vs. Ridge (03)	0	0.9	0.641
	Fen vs. Heath vs. Ridge (04)	0	0.6	0.734
	2003 vs. 2004 (Fen)			
	2003 vs. 2004 (Heath)	0	*	*
	2003 vs. 2004 (Ridge)	0	26.0	0.899

4.2.10 Vaccinium vitis-idaea

The dates of first occurrence of the four phenophases that were monitored for *V. vitis-idaea* are depicted in Figure 4-22. The results of the statistical analyses of these data are displayed in Table 4-10.

As with *T. pusilla*, the phenophases observed for *V. vitis-idaea* all occurred later in the year than those of the other species, with no conspicuous phases occurring until the middle of June each year. There were no significant phenological differences at all between treatments, but the timing of flower bud burst and flowering both differed significantly between years. Flower bud burst occurred nearly a month later in 2004 than it had in 2003. Similarly, flowering occurred around two weeks later in 2004.

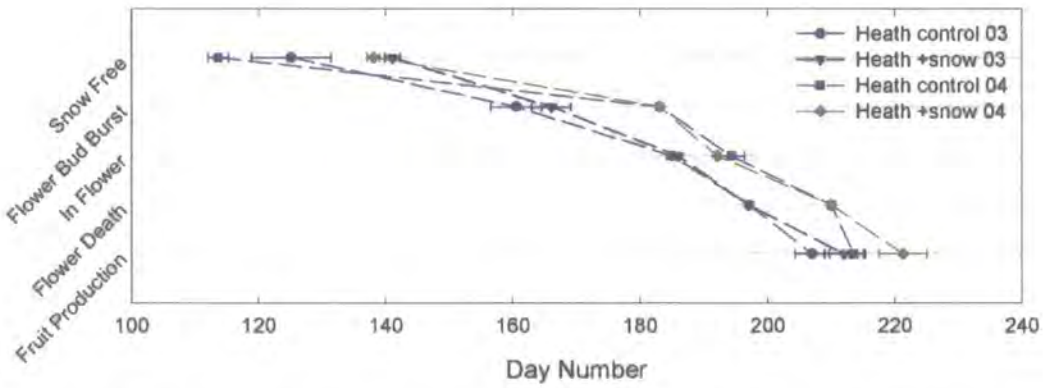

Figure 4-22: Mean dates of phenophase first occurrence for *V. vitis-idaea* (± standard error).

Table 4-10: Results of statistical analyses of phenology data for *V. vitis-idaea*.

Phenophase	Comparison	Difference	*W*	*P*
Flower Bud Burst	control vs. +snow (Heath 03)	0	14.0	0.589
	control vs. +snow (Heath 04)	0	*	*
	2003 vs. 2004 (Heath)	– +	*	*
In Flower	control vs. +snow (Heath 03)	0	*	*
	control vs. +snow (Heath 04)	0	*	*
	2003 vs. 2004 (Heath)	– +	10.0	0.023
Flower Death	control vs. +snow (Heath 03)	0	*	*
	control vs. +snow (Heath 04)			
	2003 vs. 2004 (Heath)			
Fruit Production	control vs. +snow (Heath 03)	0	13.5	0.414
	control vs. +snow (Heath 04)	0	13.0	0.134
	2003 vs. 2004 (Heath)	0	12.0	0.099

4.2.11 Image Analysis

In each community there was a clear seasonal trend in average plot greenness (see Figure 4-23), with index values increasing through June, peaking in July/August, and then dropping off again towards the end of the growing season. This seasonal trend is less pronounced in the Ridge community due to the relative sparseness of the vegetation cover compared to the Fen or Heath. Nevertheless, a significant effect of survey date was observed for all three communities (F=13.84, 35.36, 5.06; P<0.001, <0.001, <0.001; for the Fen Heath and Ridge communities respectively).

No significant differences in greenness were observed between treatments in any of the three study communities (F=0.36, 0.39, 0.27; P=0.568, 0.551, 0.616). In the Fen and Heath communities, there was no interaction between survey date and

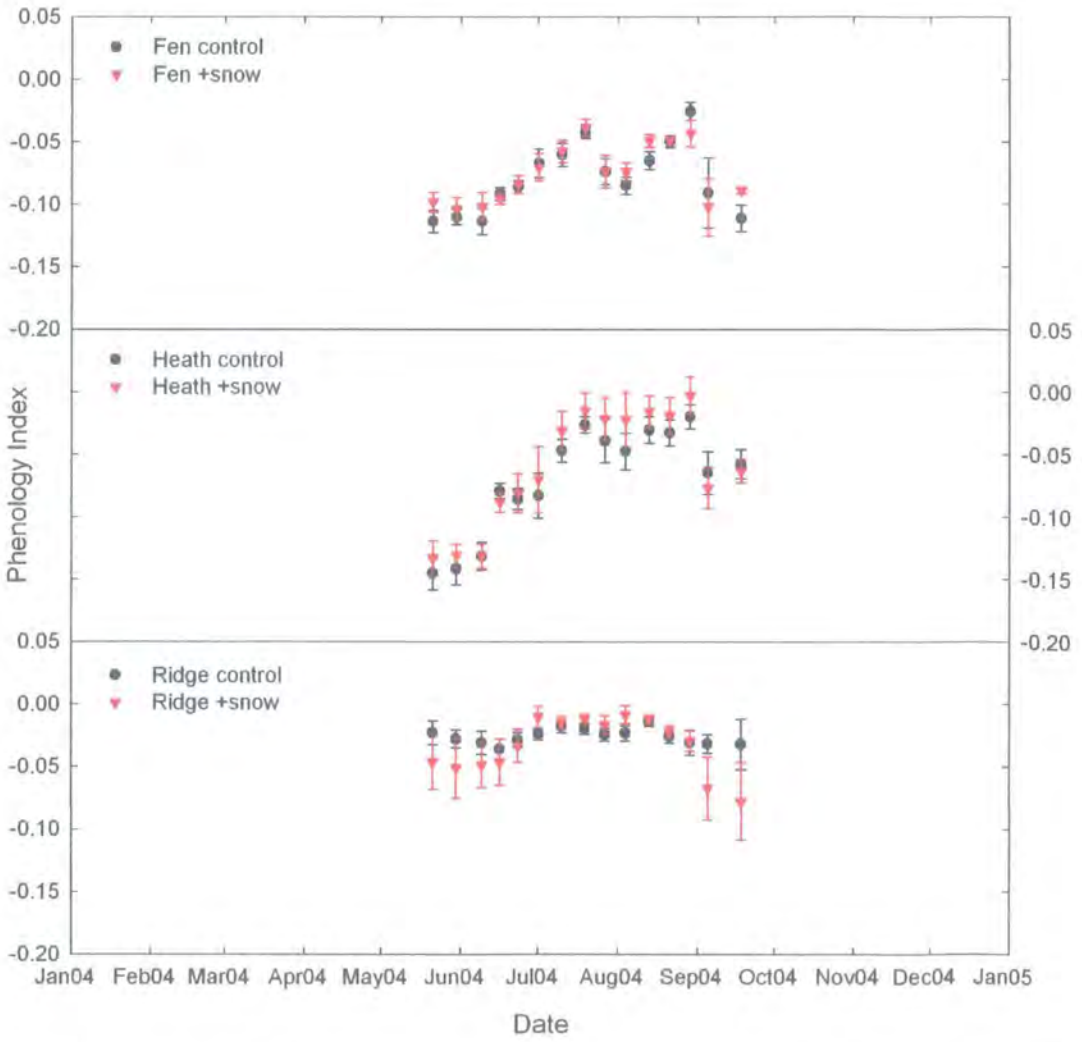

Figure 4-23: Mean study plot foliar phenology index (± standard error; n=5).

treatment effect either (F=0.63, 0.53; P=0.833, 0.913), indicating the absence of any influence of the treatment on the timing of average community greening/de-greening. In the Ridge community however, there does appear to have been a significant interaction between survey date and treatment (F=2.33, P=0.007).

The foliar phenology index was found to differ significantly between the 'control' plots of the three communities (F=16.37, P<0.001), with a significant interaction between survey date and community type (F=7.37, P<0.001). This indicates absolute differences in greenness between the communities, as well as variability in the rates at which greening/de-greening occur.

4.3 PLANT PERFORMANCE

4.3.1 Stem Growth

E. hermaphroditum annual stem growth increments typically ranged between 12 and 25 mm, with considerable natural interannual variability (see Figure 4-24). Having corrected for natural interannual variability, no significant differences in '+snow' treatment *E. hermaphroditum* growth were found between 2002 (immediately before the start of the experiment) and 2003 (the first year after manipulations began) in any of the three communities (t=-2.30, 0.62, 1.46; P=0.083, 0.568, 0.218; for the Fen, Heath and Ridge communities respectively) (see Figure 4-25).

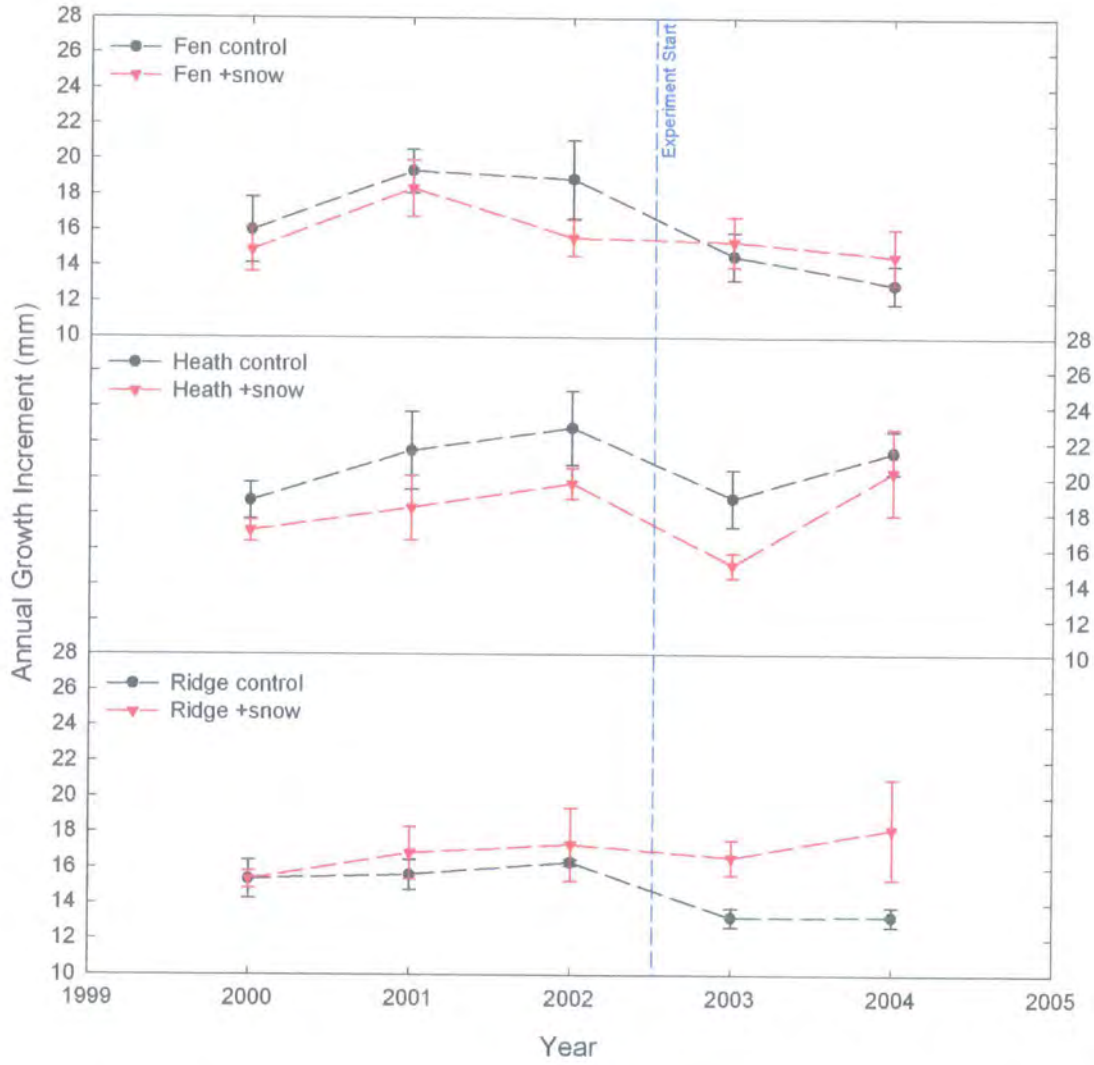

Figure 4-24: Mean annual stem growth for *E. hermaphroditum* (± standard error; n=5).

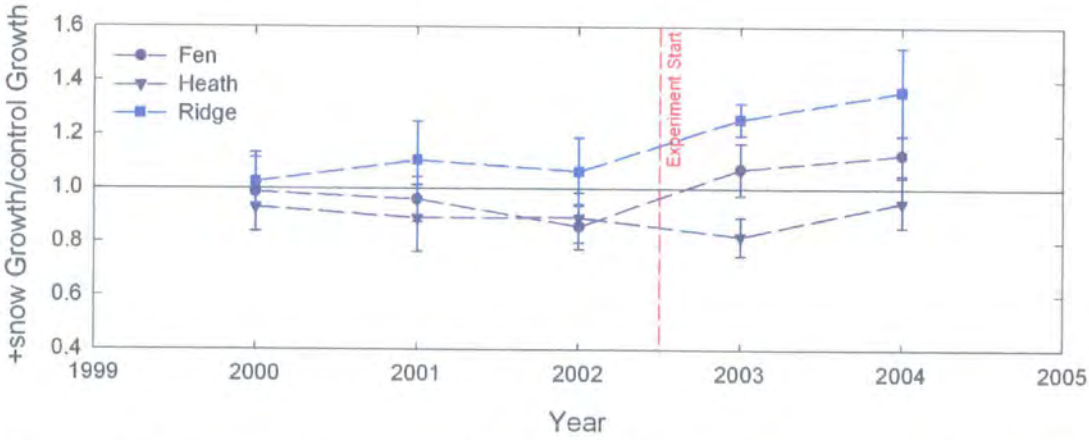

Figure 4-25: Mean annual stem growth index for *E. hermaphroditum* (± standard error; n=5).

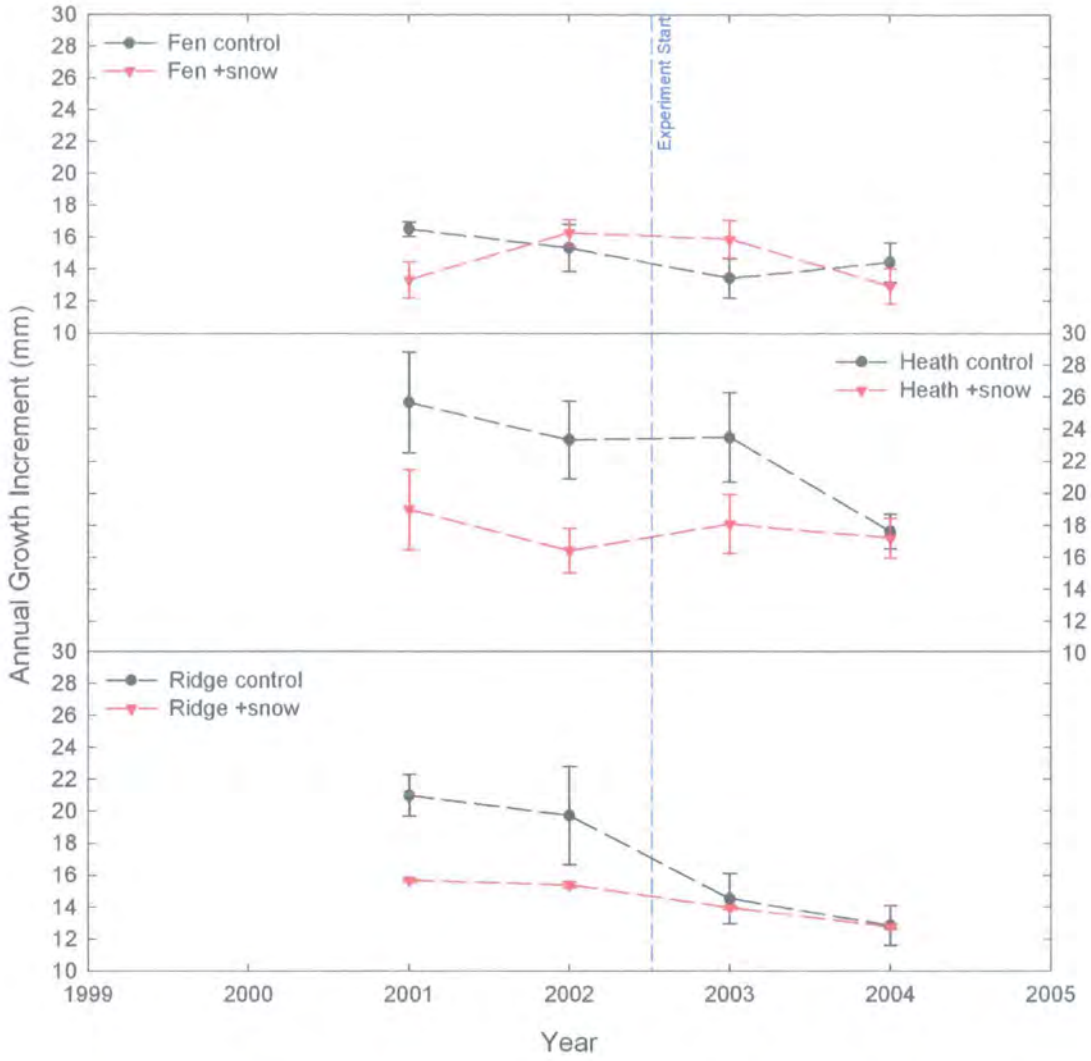

Figure 4-26: Mean annual stem growth for *V. uliginosum* (± standard error; n=5).

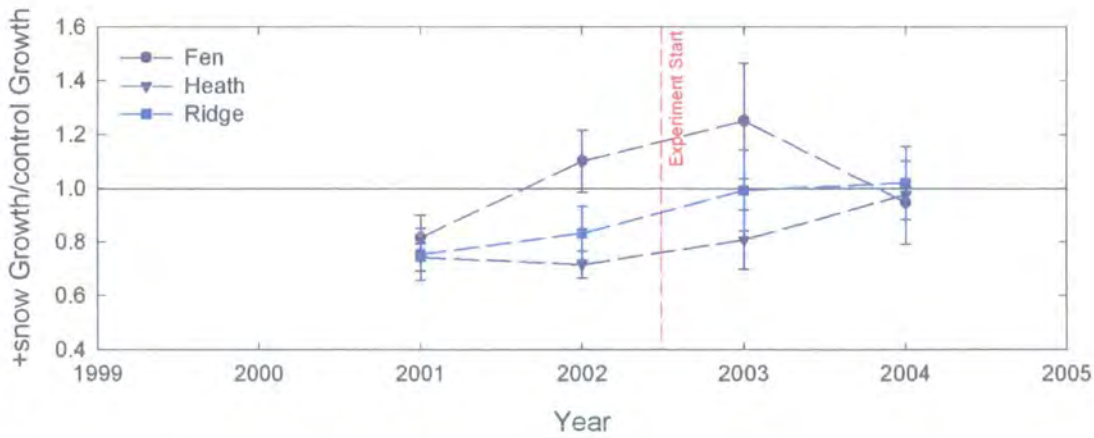

Figure 4-27: Mean annual stem growth index for *V. uliginosum* (± standard error; n=5).

Although there were still no significant differences between 2002 and 2004 in the Fen and Heath communities, there was a significant difference between the two years in the Ridge (t=-2.50, -0.33, -4.62; P=0.067, 0.755, 0.010), where growth was approximately 25% greater after two years of manipulation than before.

V. uliginosum annual stem growth increments ranged between 11 and 29 mm, with considerable natural interannual variability and, in both the Heath and Ridge communities, considerable differences between the 'control' and '+snow' treatments apparent prior to the implementation of any manipulations (see Figure 4-26). As before, no significant differences in *V. uliginosum* growth were found between 2002 and 2003 in any of the three communities (t=-0.91, -1.09, -1.42; P=0.415, 0.337, 0.228; for the Fen, Heath and Ridge communities respectively) (see Figure 4-27). Although there were still no significant differences between 2002 and 2004 in the Fen and Ridge communities, there was a significant difference between the two years in the Heath (t=0.96, -4.48, -1.58; P=0.390, 0.011, 0.190), where growth was approximately 40% greater after two years of manipulation than before.

For both species there was a significant difference in average annual stem growth increment (over the five/four year period for which measurements were taken) between the 'controls' of the three communities (F=9.86, 7.55; P=0.003, 0.008; for *E. hermaphroditum* and *V. uliginosum* respectively), with more growth per year on average in the Heath community than in the Fen (t=-2.60, -3.79; P=0.035, 0.013), and more growth in the Heath than in the Ridge (t=4.91, 2.38; P=0.008,

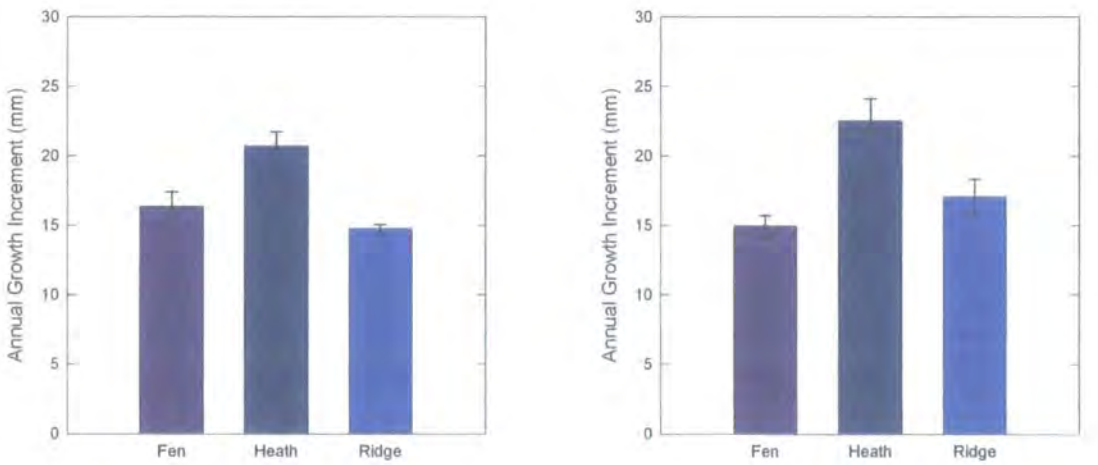

Figure 4-28: Five-year average annual stem growth for *E. hermaphroditum* (left) and four-year average annual stem growth for *V. uliginosum* (right) (± standard error; n=5).

0.049) (see Figure 4-28). There were no significant differences between the Fen and the Ridge communities for either species (t=1.32, -1.24; P=0.257, 0.261).

4.3.2 Branching

For *E. hermaphroditum*, the number of new branches formed each year typically ranged between one and three, with some natural interannual variability (see Figure 4-29). Having corrected for this natural interannual variability, no significant differences in '+snow' treatment *E. hermaphroditum* branching were found between 2002 (immediately before the start of the experiment) and 2003 (the first year after manipulations began) in any of the three communities (t=-0.61, -0.37, 0.00; P=0.576, 0.733, 0.999; for the Fen, Heath and Ridge communities respectively) (see Figure 4-30). Nor were any significant differences found between 2002 and 2004 (t=-0.91, 1.95, 0.81; P=0.415, 0.124, 0.463).

For *V. uliginosum*, the number of new branches formed each year ranged between zero and two, with considerable natural interannual variability (see Figure 4-31). Having corrected for this natural interannual variability, no significant differences in *V. uliginosum* branching index were found between 2002 and 2003 in any of the three communities (t=-0.03, 1.19, -0.44; P=0.979, 0.299, 0.682; for the Fen, Heath and Ridge communities respectively) (see Figure 4-32). Although there were still no significant differences between 2002 and 2004 in the Fen and Ridge communities, there was a significant difference between the two years in the Heath (t=1.88, 2.84, -2.45; P=0.133, 0.047, 0.070), where branching was approximately 50% less frequent after two years of manipulation than before. However, the *V. uliginosum* corrected branching index displays considerable variability between years prior to the start of the experiment.

For both species there was a significant difference in the average annual branching frequency (over the five/four year period for which measurements were made) between the 'controls' of the three communities (F=9.40, 6.07; P=0.003, 0.015; for *E. hermaphroditum* and *V. uliginosum* respectively), with more new branches per year on average in the Ridge community than in the Fen for both species (t=-4.34, -9.93; P=0.007, 0.001), and more new branches in the Heath community than in the Fen for *E. hermaphroditum* (t=-3.31, -2.13; P=0.013, 0.101) (see Figure 4-33). There were no significant differences between the Heath and Ridge communities for either species (t=0.27, -0.60; P=0.797, 0.581).

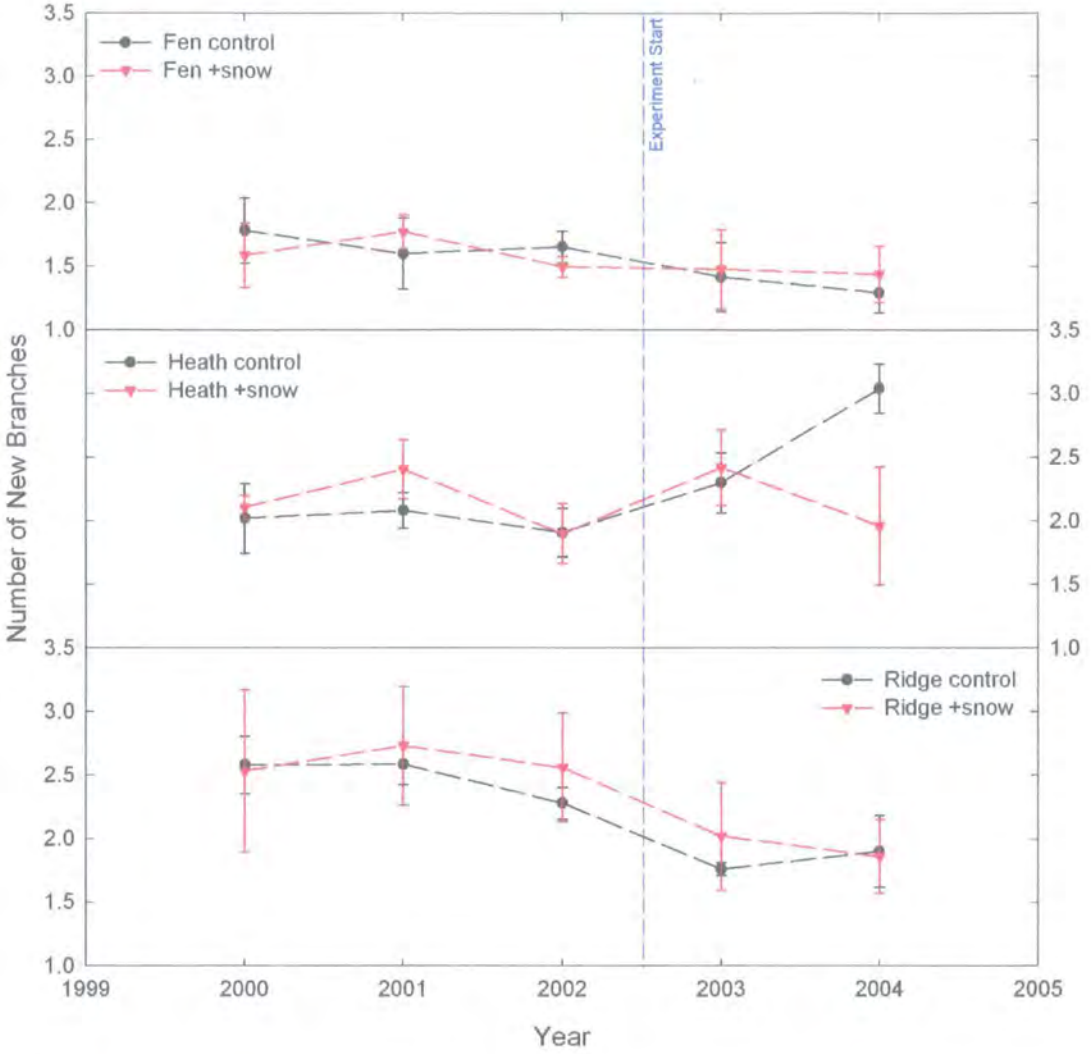

Figure 4-29: Mean annual branching frequency for *E. hermaphroditum* (± standard error; n=5).

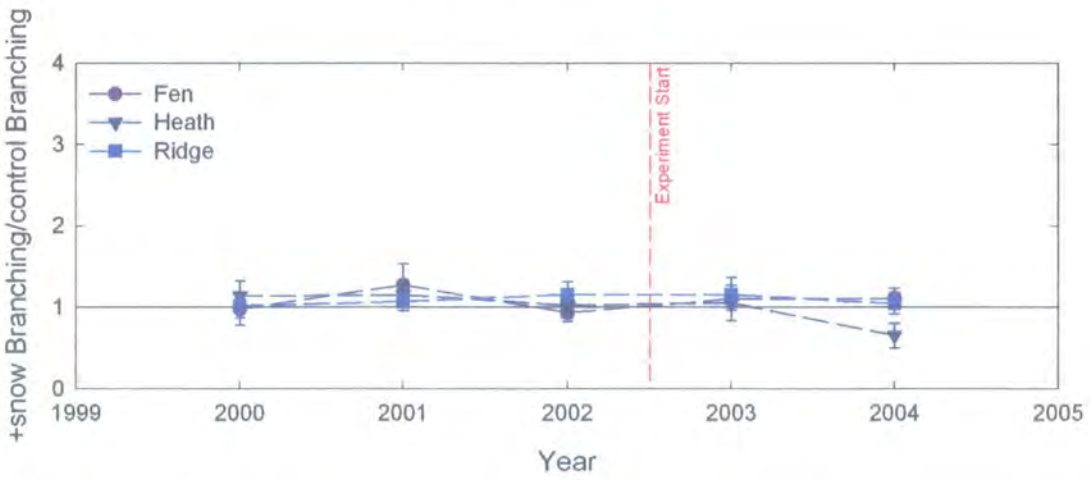

Figure 4-30: Mean annual branching index for *E. hermaphroditum* (± standard error; n=5).

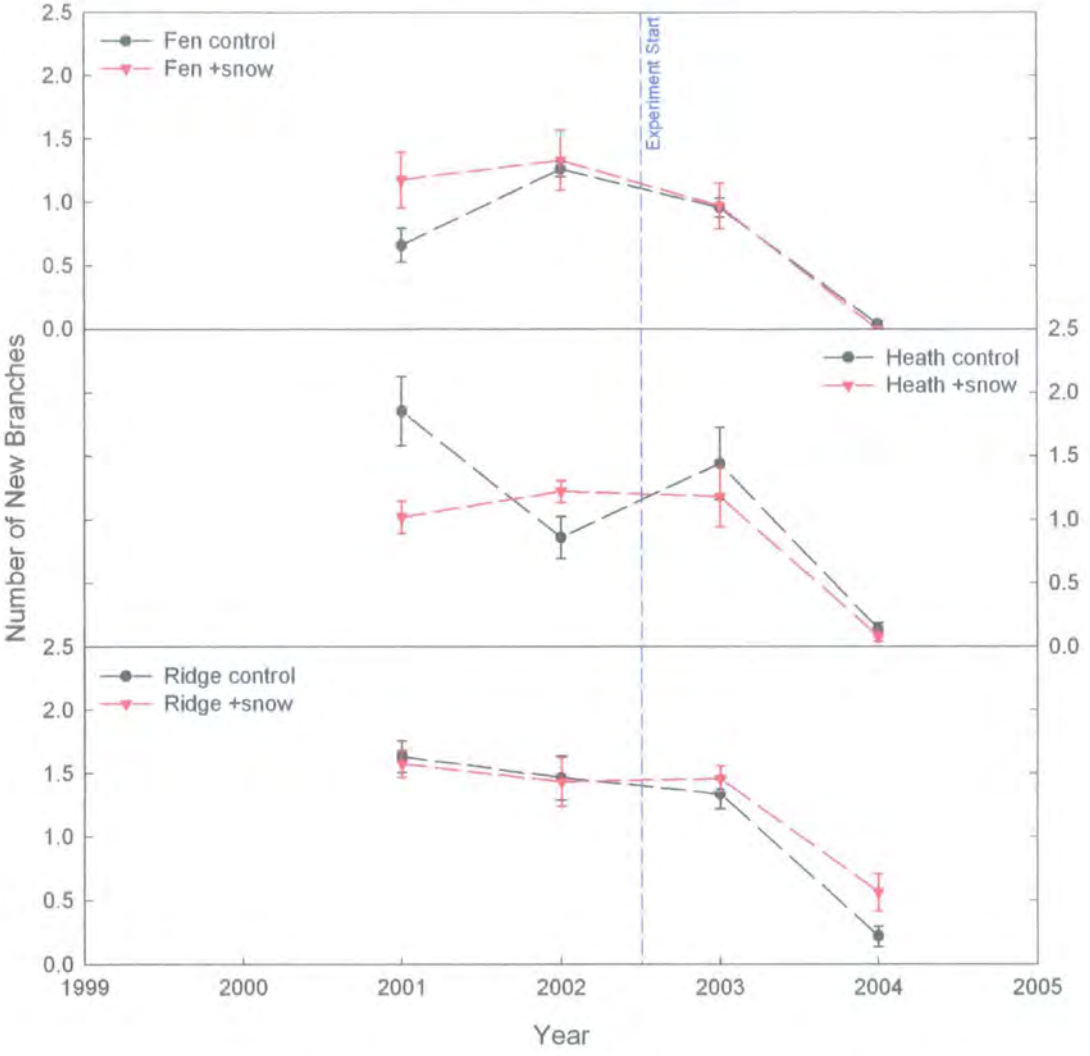

Figure 4-31: Mean annual branching frequency for *V. uliginosum* (± standard error; n=5).

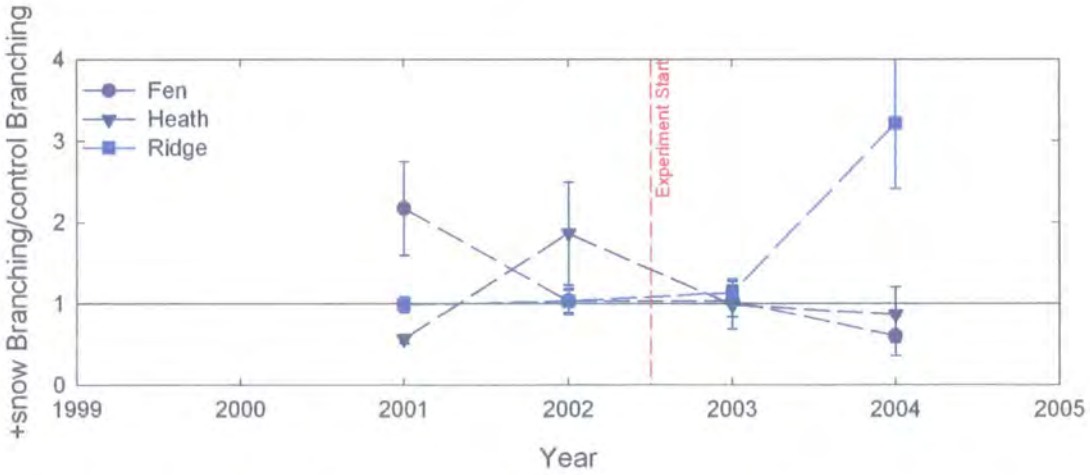

Figure 4-32: Mean annual branching index for *V. uliginosum* (± standard error; n=5).

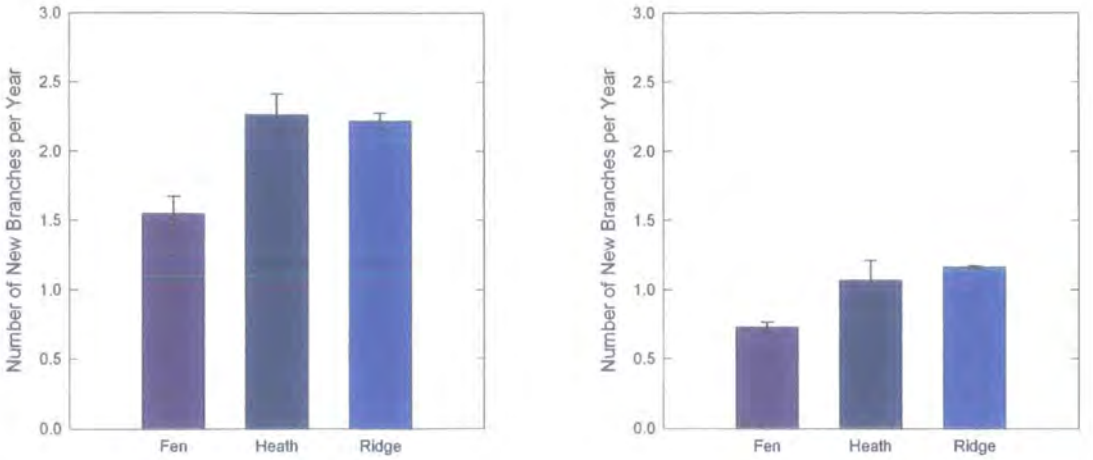

Figure 4-33: Five-year average annual branching frequency for *E. hermaphroditum* (left) and four-year average branching frequency for *V. uliginosum* (right) (± standard error; n=5).

4.3.3 Leaf Growth

For *B. nana*, average leaf area was found to be in the region of 0.6 to 0.9 cm^2 per leaf, with no significant differences between treatments (t=-0.82, -0.49, -0.69; P=0.440, 0.640, 0.510; for the Fen, Heath and Ridge communities respectively) or communities (F=0.25, P=0.782) (see Figure 4-34). Average leaf weight ranged from 9 to 15 mg per leaf and, as with leaf area, did not differ significantly between treatments (t=-1.59, 1.01, 0.08; P=0.155, 0.347, 0.937) or communities (F=2.00, P=0.178).

For *V. uliginosum* average leaf area was generally smaller than that observed for *B. nana*, ranging from 0.5 to 0.8 cm^2 per leaf (see Figure 4-35). Although no

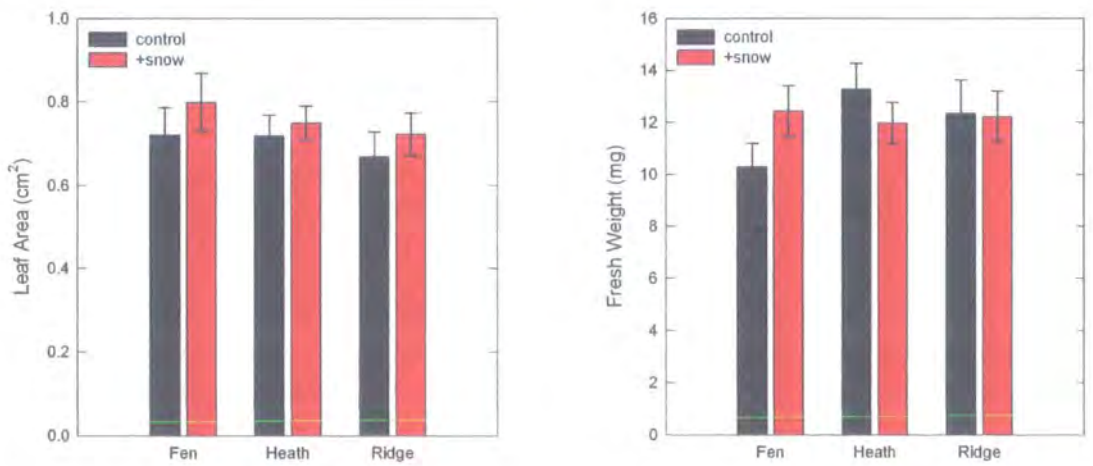

Figure 4-34: Mean leaf area (left) and weight (right) for *B. nana* (± standard error; n=5). Values are per leaf.

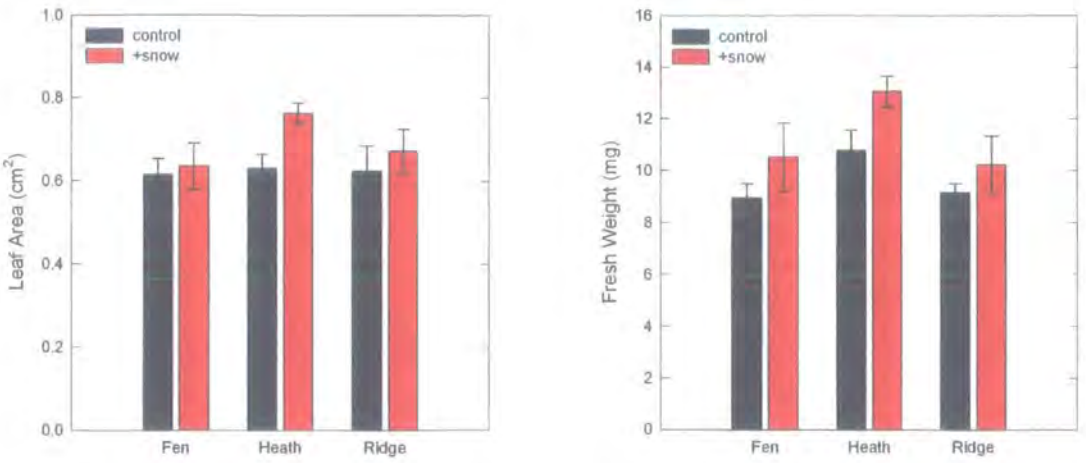

Figure 4-35: Mean leaf area (left) and weight (right) for *V. uliginosum* (± standard error; n=5). Values are per leaf.

significant differences between treatments were found in the Fen or Ridge communities, leaf area was found to be significantly greater (~15%) in the '+snow' treatment than in the 'control' in the Heath community (t=-0.30, -3.11, -0.60; P=0.769, 0.017, 0.565; for the Fen, Heath and Ridge communities respectively). There was no significant difference in leaf area between any of the communities (F=0.03, P=0.975). *V. uliginosum* leaf weights were also slightly lighter than those of *B. nana* and, in concordance with the leaf area data, were found to be approximately 15% greater (nearly significant) in the '+snow' treatment than in the 'control' in the Heath community alone (t=-1.11, -2.35, -0.95; P=0.317, 0.051, 0.396), with no significant differences between communities (F=2.96, P=0.090).

4.3.4 Leaf Nutrient Content

B. nana leaves typically contained between 18 and 26 mg N g^{-1} dry weight, with significantly less nitrogen (~20%) in the '+snow' treatment than in the control in the Fen community (t=2.86, P=0.036), but no significant differences in the Heath (W=28.0, P=1.000) or Ridge (t=0.44, P=0.677) (see Figure 4-36). Nitrogen content was found to be considerably lower in *E. hermaphroditum* leaves than those of *B. nana* (~8 to 15 mg N g^{-1} dry weight). In the Fen and Heath communities, they contained significantly more nitrogen (~20%) in the '+snow' treatments than in the 'controls' (t=-3.14, -2.49; P=0.020, 0.047; for the Fen and Heath communities respectively), whereas in the Ridge, leaf nitrogen was significantly lower (~25%) in the '+snow' treatment (W=40.0, P=0.012). The leaves of *V. uliginosum* were more similar to *B. nana* than *E. hermaphroditum* in terms of their nitrogen content (~17 to

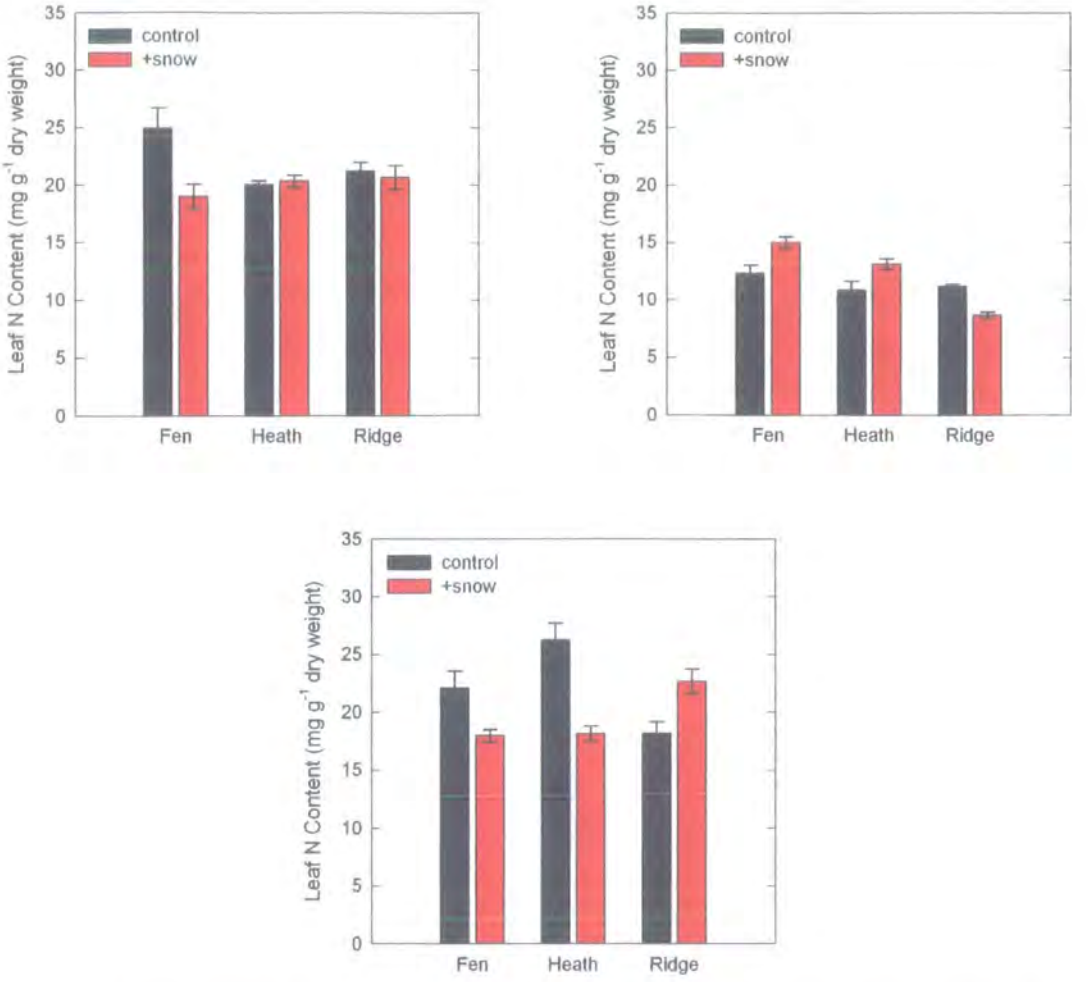

Figure 4-36: Mean leaf nitrogen contents for *B. nana* (top left), *E. hermaphroditum* (top right) and *V. uliginosum* (bottom) (± standard error; n=5).

27 mg N g^{-1} dry weight). Interestingly, their response to the '+snow' treatment was opposite to that observed in *E. hermaphroditum*, with significantly lower nitrogen contents (~20 to 30%) in the '+snow' treatments than in the 'controls' in the Fen (T=2.65, P=0.045) and Heath (t=5.02, P=0.004) communities, and significantly higher nitrogen contents (25%) in the '+snow' treatment in the Ridge (t=-3.15, P=0.016).

Although leaf nitrogen content did not differ significantly between communities for *E. hermaphroditum* (F=1.52, P=0.259), significant community differences were found for *B. nana* (F=5.98, P=0.017), where leaf nitrogen concentrations were greater in the Fen than in the Heath, and *V. uliginosum* (F=9.23, P=0.004), where they were greater in the Heath than in the Ridge.

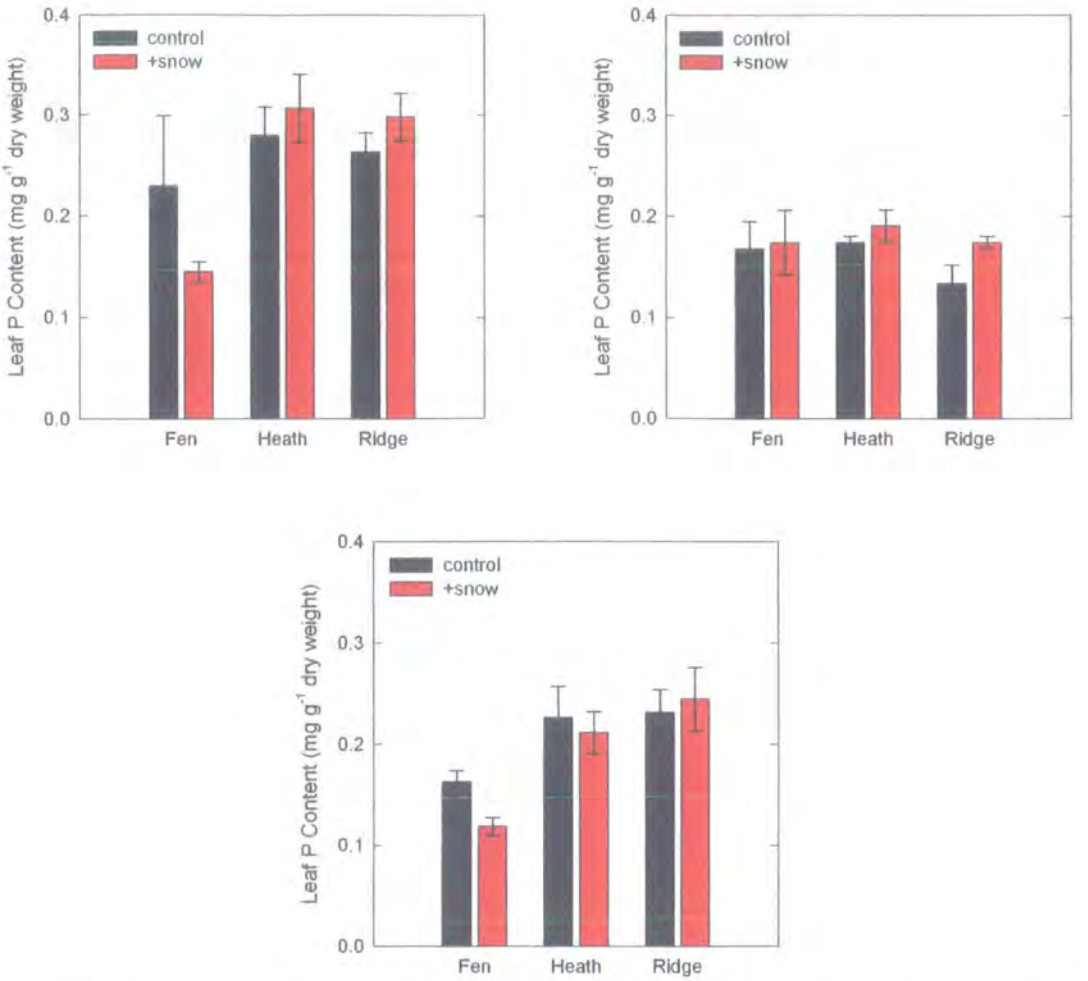

Figure 4-37: Mean leaf phosphorus contents for *B. nana* (top left), *E. hermaphroditum* (top right) and *V. uliginosum* (bottom) (± standard error; n=5).

Leaf phosphorus concentrations were around two orders of magnitude lower than those of nitrogen, with values typically ranging from 0.12 to 0.32 mg P g^{-1} dry weight (see Figure 4-37). There were also far fewer significant differences in leaf phosphorus content between treatments than were found for leaf nitrogen, with no significant differences at all for *B. nana* (W=34.0, t=-0.61, -1.14; P=0.189, 0.561, 0.292; for the Fen, Heath and Ridge communities respectively) or *E. hermaphroditum* (t=-0.16, -0.96, -2.11; P=0.880, 0.380, 0.103). For *V. uliginosum*, leaf phosphorus was significantly lower (~25%) in the '+snow' treatment than in the 'control' in the Fen community (t=3.09, P=0.018), but there was no difference between treatments in the Heath (t=0.40, P=0.704) or Ridge (t=-0.34, P=0.744). Leaf phosphorus content was not found to differ significantly between any of the

three communities for *B. nana* (H=3.39, P=0.184), *E. hermaphroditum* (F=1.31, P=0.307) or *V. uliginosum* (F=2.80, P=0.100).

4.3.5 Flowering

Significantly fewer (~60%) *A. polifolia* flowers per percent coverage were observed in the '+snow' treatment than in the 'control' in the Fen community (T=2.53, P=0.039), but not in the Heath (W=12.0, P=0.149), where the sample size was small due to the infrequent occurrence of *A. polifolia* in the +snow plots (see Figure 4-38). No significant differences between treatments were observed in any of the communities for *B. nana* (W=25.5, 13, 7; P=1.000, 0.191, 0.773; for the Fen, Heath and Ridge communities respectively) or *V. uliginosum* (W=34.0, 26.0, 21.0; P=0.189, 0.834, 0.902).

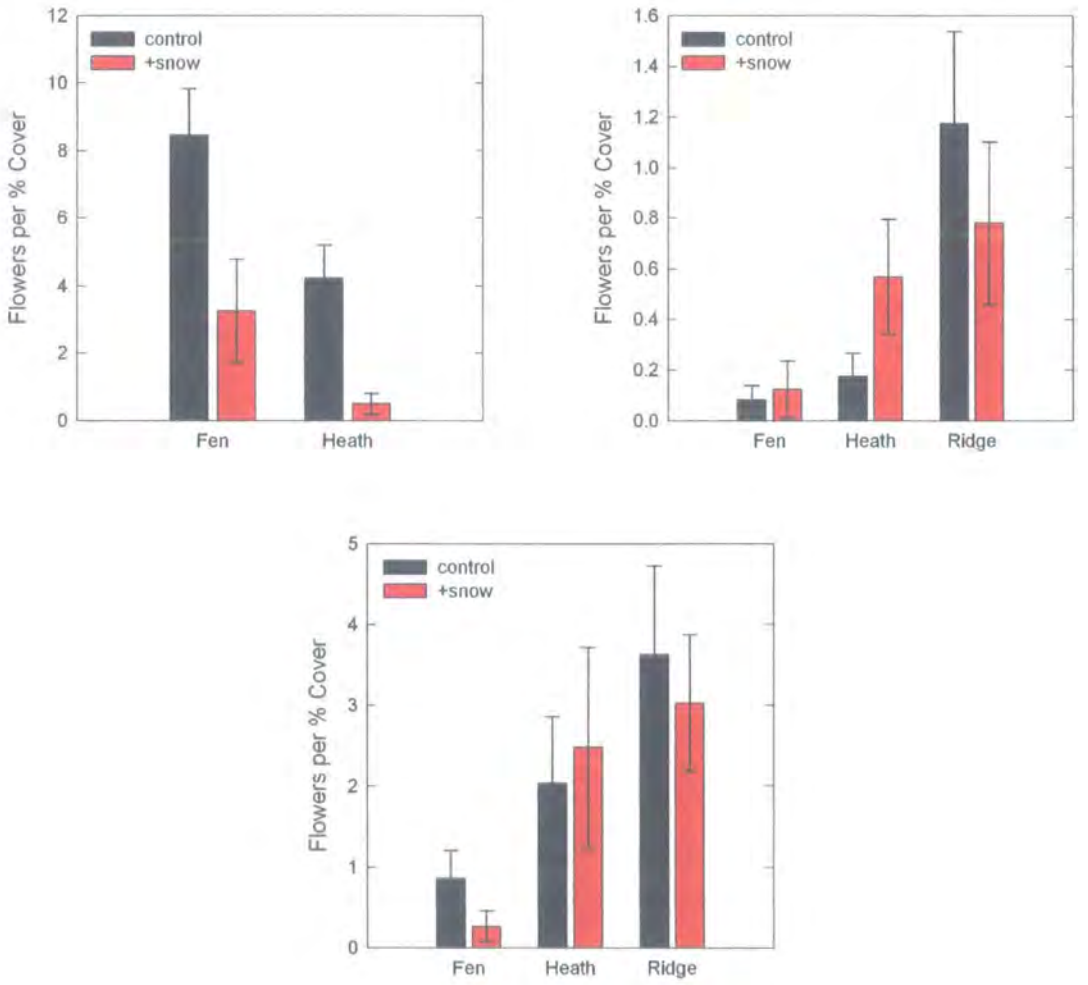

Figure 4-38: Mean flowering frequencies for *A. polifolia* (top left), *B. nana* (top right) and *V. uliginosum* (bottom) (± standard error).

The flowering frequency of *A. polifolia* did not differ significantly between the two communities in which this species occurs (W=8.0, P=0.136), with flowering frequencies ranging from three to ten flowers per percent cover and considerable variability between plots. The number of *B. nana* and *V. uliginosum* flowers however, did differ significantly between communities (H=7.26, 10.42; P=0.027, 0.005), with more flowers in the Ridge community than in the Fen or Heath in each case.

4.3.6 Fruit Production

No significant differences between treatments were observed for any of the species in either the Fen (W=35.5, *, 26.0, 30.0; P=0.094, *, 0.884, 0.601; for *A. polifolia*, *B. nana*, *E. hermaphroditum* and *V. uliginosum* respectively), Heath (W=*, 15.0, 27.0, 24.0; P=*, 0.408, 1.000, 0.441) or Ridge (W=7.5, 13.0, 21.0; P=0.554, 0.860, 0.867;

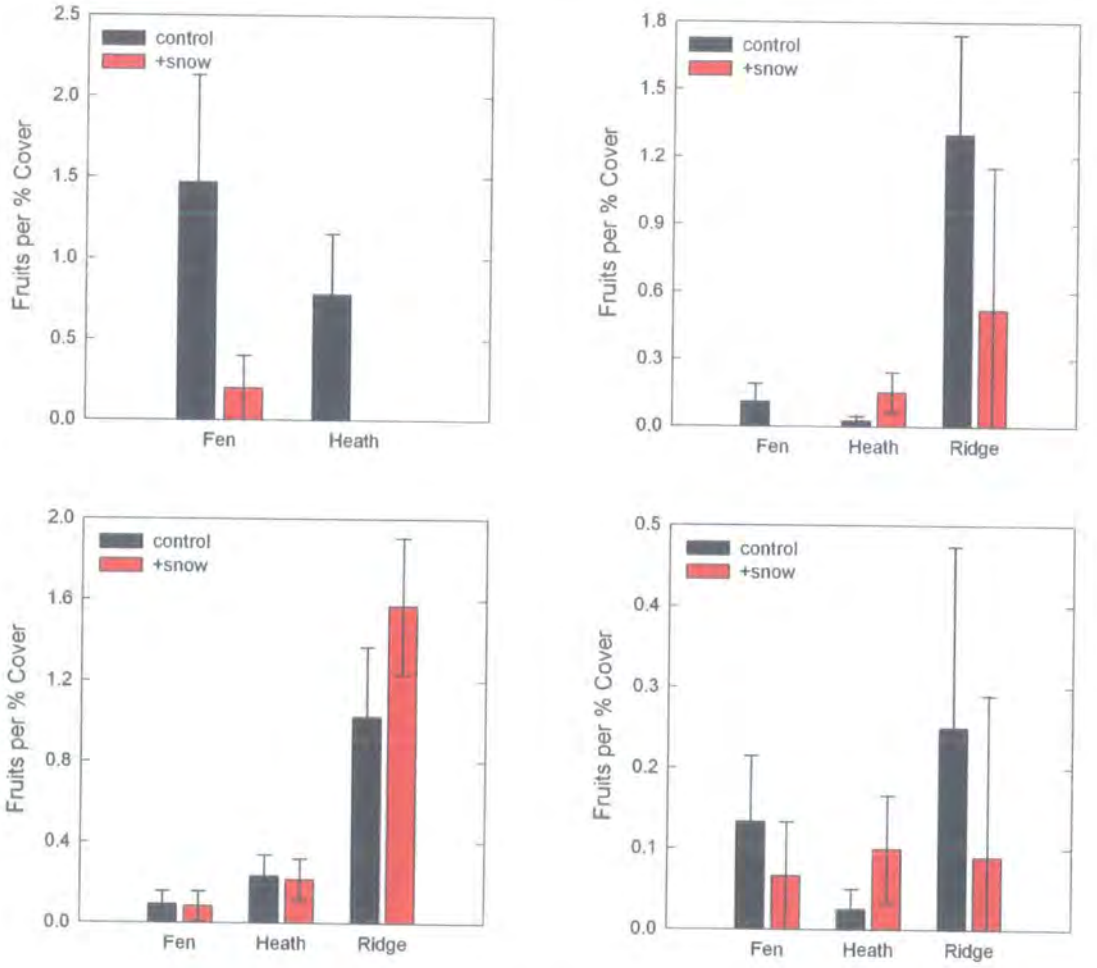

Figure 4-39: Mean fruiting frequencies for *A. polifolia* (top left), *B. nana* (top right), *E. hermaphroditum* (bottom left) and *V. uliginosum* (bottom right) (± standard error).

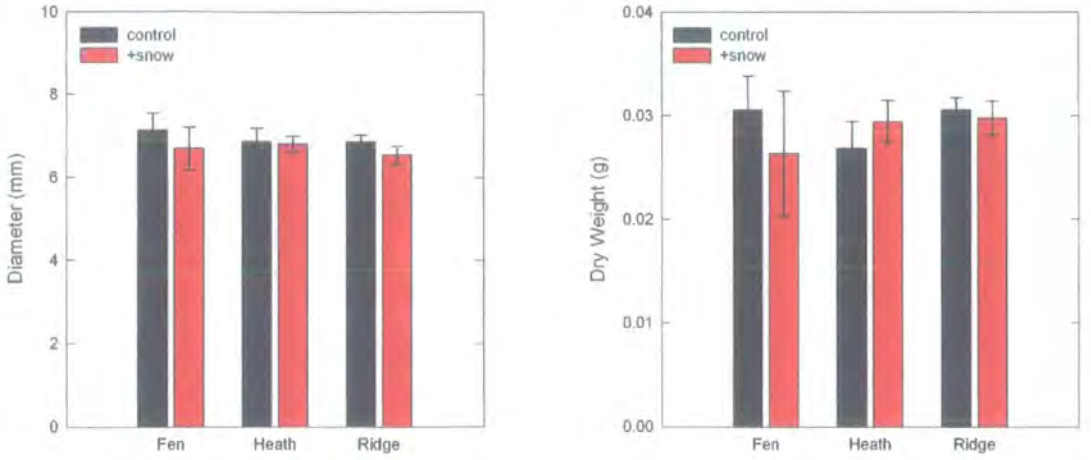

Figure 4-40: Mean berry diameter (left) and weight (right) for *E. hermaphroditum* (± standard error; n=5).

for *B. nana*, *E. hermaphroditum*, and *V. uliginosum* respectively) communities (see Figure 4-39). However, as indicated by the *, it was not possible to perform the relevant statistical test for *B. nana* in the Fen community or *A. polifolia* in the Heath, due to the fact that no fruits were produced in any of the +snow plots in either case. This absence of fruits could possibly be interpreted as a significant treatment effect.

The frequency of fruit production did not differ significantly between communities for *A. polifolia* (W=24.5, P=0.655) or *V. uliginosum* (H=0.04, P=0.978), ranging from 0.25 to 2.25 and 0 to 0.5 fruits per percent cover respectively, with considerable variation between plots in each case. Fruit production frequency did however differ significantly between communities for *B.*

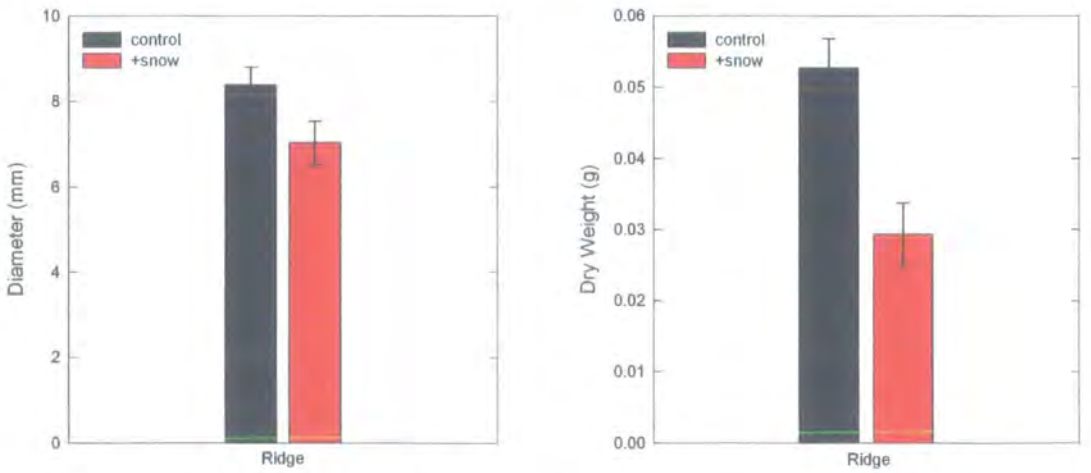

Figure 4-41: Mean berry diameter (left) and weight (right) for *V. uliginosum* (± standard error; n=5).

nana (H=7.84, P=0.020) and *E. hermaphroditum* (H=8.90, P=0.012), with up to 2500% and 900% more fruits per percent cover in the Ridge community than in the Fen or Heath for each species respectively.

There were no significant differences in berry diameter between treatments for either *E. hermaphroditum* or *V. uliginosum* in the Fen (t=0.68, P=0.519; no *V. uliginosum* data due to lack of berries), Heath (t=0.13, P=0.903; again, no *V. uliginosum* data due to lack of berries) or Ridge (t=1.16 2.04; P=0.283, 0.080; for *E. hermaphroditum* and *V. uliginosum* respectively) communities, with berry diameters ranging from approximately 6 to 7.5 mm and 6.5 to 9 mm for each species respectively (see Figure 4-40 and Figure 4-41). Nor were there any significant differences between communities (F=0.26, P=0.776; for *E. hermaphroditum*).

For *E. hermaphroditum*, there were also no significant differences in berry weight between treatments in any of the communities (W=35.0, 23.0, t=0.43; P=0.144, 0.403, 0.679; for the Fen, Heath and Ridge communities respectively), with weights typically ranging from approximately 0.025 to 0.035 g (see Figure 4-40). Nor were there any significant differences between communities (F=0.76, P=0.487). For *V. uliginosum* however, there was a significant difference in berry weight between treatments in the one community in which it was observed; the Ridge (t=3.80, P=0.007), where the berries were approximately 45% lighter in the '+snow' treatment than in the 'control' (see Figure 4-41).

4.4 ECOSYSTEM CARBON DIOXIDE EXCHANGE

4.4.1 The Fen

On any given day there was often a high degree of variability between plots of the same treatment, especially in the case of GPP (see Figure 4-42). In spite of this, it is still possible to see that there was a clear seasonal trend in both years for NEE, ER and GPP. ER and GPP values both became greater (more negative in the case of GPP) as the snow-free season progressed each year, reaching peak values around the end of July, and dropping back towards zero thereafter. Both were of a similar magnitude throughout the study period, ranging from approximately 0 to 0.9 and -1.0 g CO_2 m^{-2} hr^{-1} (for ER and GPP respectively); consequently, NEE values were rarely far from the compensation point, typically ranging from 0.2 to

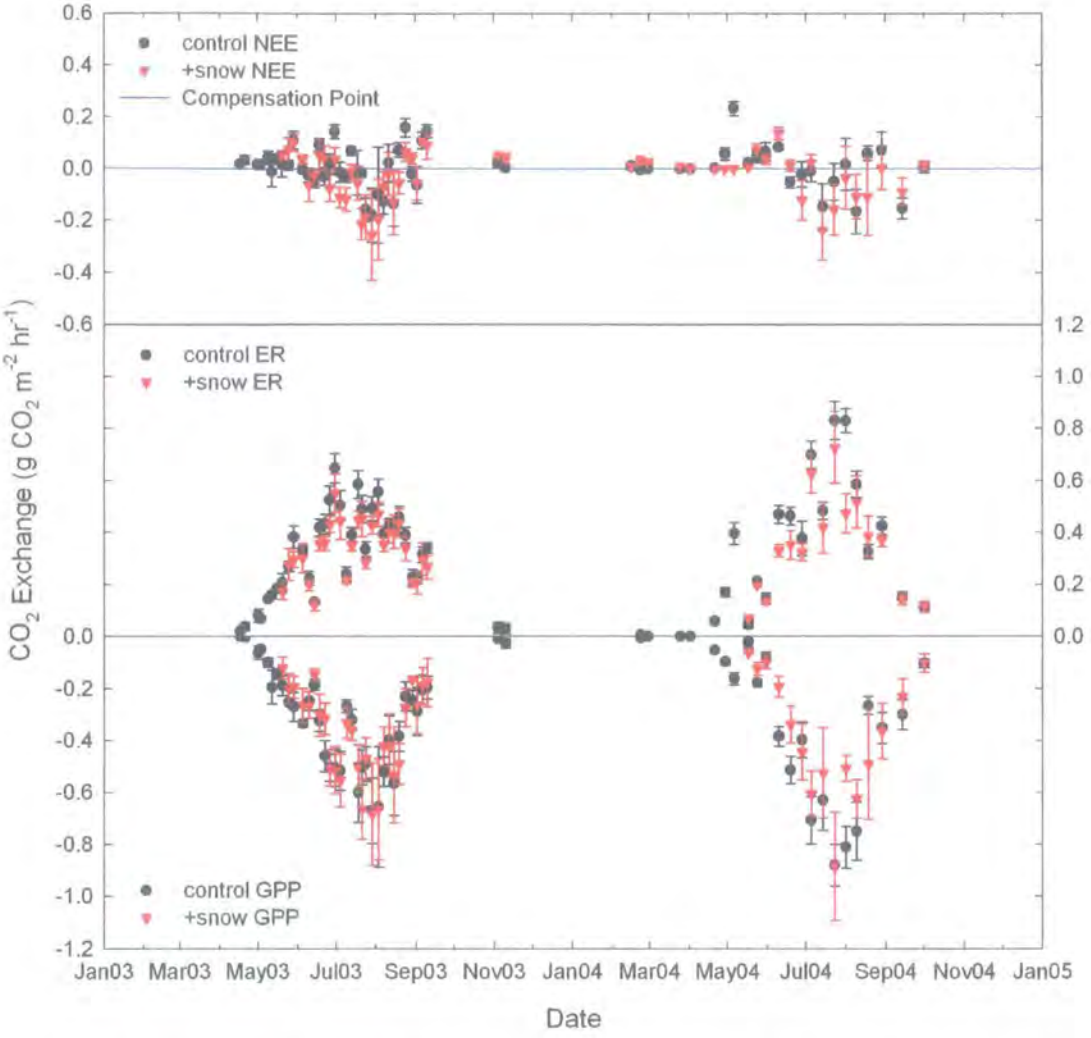

Figure 4-42: Mean study plot CO_2 exchange for the Fen community (± standard error; n=5).

-0.3 g CO_2 m^{-2} hr^{-1}. Nevertheless, a general shift from net CO_2 efflux to net assimilation was apparent around the middle of June in both years, switching back around a month later in each case.

Repeated measures ANOVA revealed no significant differences in NEE (F=0.51, 0.22; P=0.494, 0.648; for 2003 and 2004 respectively), ER (F=1.53, 2.40; P=0.251, 0.160) or GPP (F=0.01, 0.42; P=0.939, 0.538) between treatments in either year. The test did, however, reveal significant differences between sample days for each variable in both years (F=6.45, 3.62, 25.48, 34.57, 12.10, 16.99; P<0.001, <0.001 <0.001, <0.001, <0.001, <0.001; for NEE03, NEE04, ER03, ER04 GPP03 and GPP04 respectively), but no interaction between sample day and treatment except with ER in 2004 (F=0.79, 0.83, 0.58, 2.29, 0.56, 1.62; P=0.752, 0.610, 0.944, 0.016, 0.955, 0.108).

Analysis of the linear relationships between the control and +snow data did expose significant differences between the two treatments (Figure 4-43 and Table 4-11). In each case there was a significant relationship between the treatments, but for NEE, ER and GPP in 2004, the relationship was significantly different from 1:1 (as indicated by the slope test), with greater ER and GPP (more negative), but more positive NEE, in the 'control' treatment in proportion to the '+snow' treatment. In 2003, NEE was also significantly more positive in the 'control' treatment than in the '+snow' (as indicated by the Y-Intercept test).

Table 4-11: Test statistics for Fen control vs. +snow regressions.

Variable	Relationship			Y-Intercept		Slope	
	R^2	F	P	t	P	t	P
NEE 2003	0.57	35.22	<0.001	-2.43	0.022	-1.07	0.292
ER 2003	0.96	536.23	<0.001	1.68	0.105	-5.33	1.256
GPP 2003	0.85	144.11	<0.001	0.72	0.481	0.39	0.701
NEE 2004	0.33	10.52	0.004	-1.55	0.136	-2.61	0.016
ER 2004	0.88	98.65	<0.001	1.52	0.153	-3.94	0.002
GPP 2004	0.80	51.60	<0.001	-0.89	0.392	-2.20	0.047

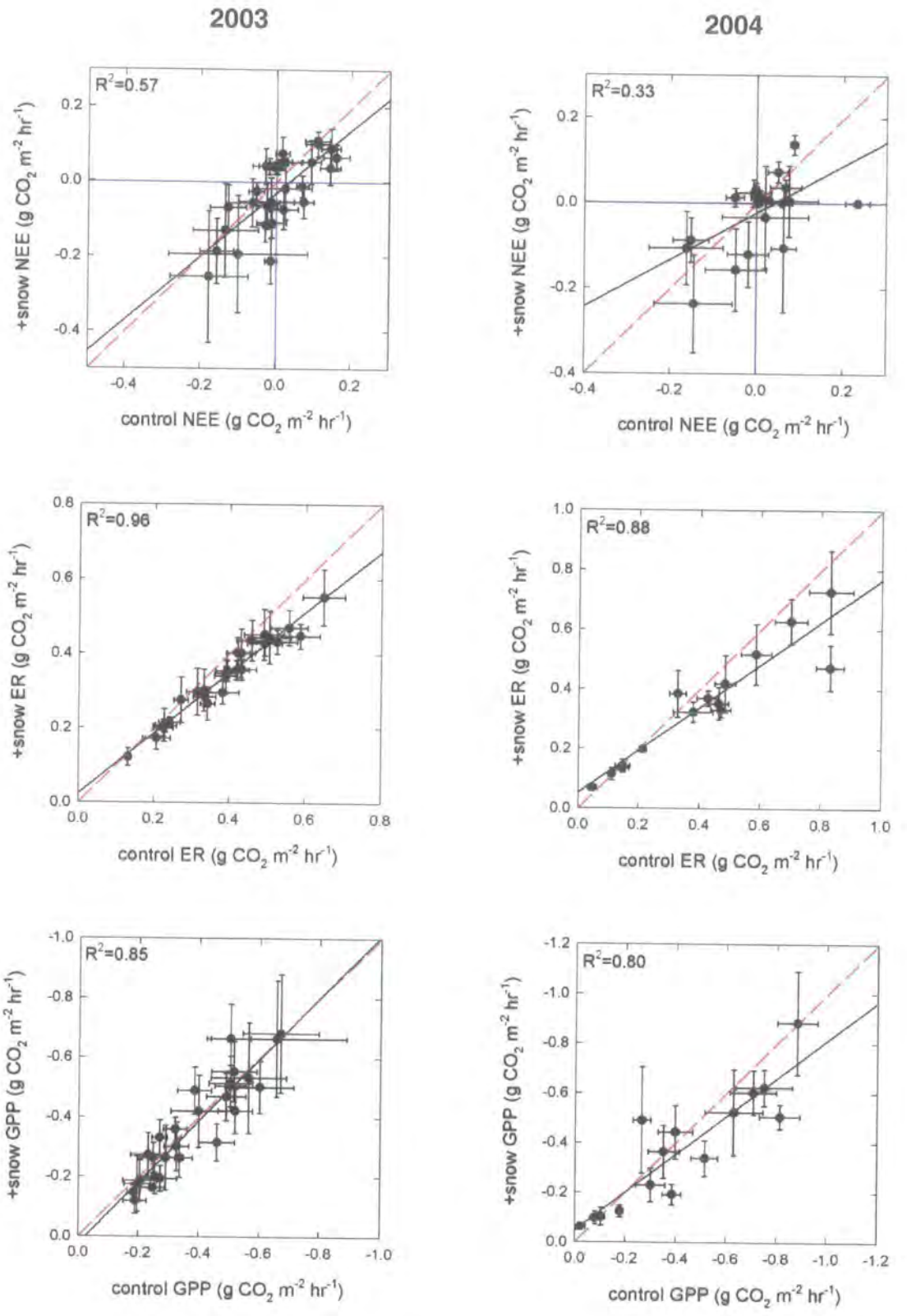

Figure 4-43: Fen 'control' vs. '+snow' treatment mean CO_2 exchange (± standard error; n=5). 2003 data are on the left and 2004 data on the right. The red dashed lines indicate the position of a 1:1 relationship while the black solid lines indicate the line of best fit. The blue solid lines on the NEE graphs indicate the compensation point.

4.4.2 *The Heath*

The root damage that was inadvertently inflicted by the collars in 2003 is clearly visible in the flux record for that year, with lower levels of both GPP and ER, but higher net CO_2 efflux overall, in comparison to 2004 (see Figure 4-44). Although it was less conspicuous in 2003, as in the Fen community, there was a clear seasonal trend in both years. In 2003, both ER and GPP became greater as the snow-free season progressed, reaching peak values in the region of 0.6 and -0.3 g CO_2 m^{-2} hr^{-1} respectively, around the beginning of July, gradually decreasing thereafter. GPP was not sufficient in that year to compensate for ER, so NEE remained positive, with values ranging from approximately 0 to 0.4 g CO_2 m^{-2} hr^{-1}. Although the general trend for ER and GPP was similar in 2004, the magnitude of the fluxes was much

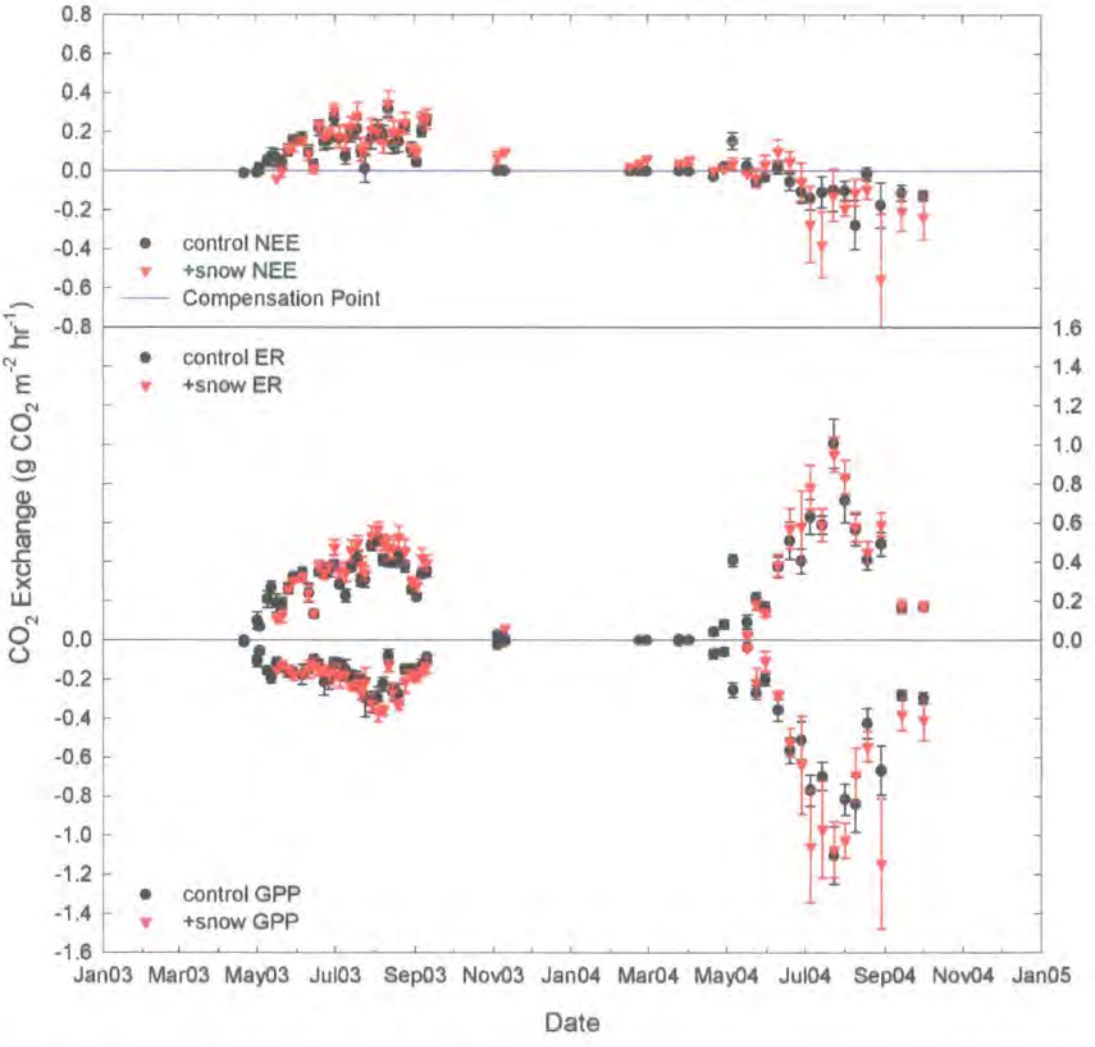

Figure 4-44: Mean study plot CO_2 exchange for the Heath community (± standard error; n=5).

greater, with peak values in the region of 1.1 and -1.4 g CO_2 m^{-2} hr^{-1} respectively. As with the Fen community data however, there was often a high degree of variability between plots of the same treatment on a given day. In 2004, GPP did reach the point where it exceeded ER, resulting in net CO_2 assimilation during all measurement periods from July onwards, with values typically ranging from 0 to -0.5 g CO_2 m^{-2} hr^{-1}.

Repeated measures ANOVA revealed no significant differences in NEE (F=0.34, 0.83; P=0.574, 0.390; for 2003 and 2004 respectively), ER (F=2.09, 0.73; P=0.186, 0.418) or GPP (F=0.46, 1.36; P=0.517, 0.276) between treatments in either year. The test did, however, reveal significant differences between sample days for all three flux variables in both years (F=11.12, 2.31, 26.16, 19.71, 8.12, 8.31; P<0.001, 0.015, <0.001, <0.001, <0.001, <0.001; for NEE03, NEE04, ER03, ER04, GPP03 and GPP04 respectively), but no interaction between sample day and treatment (F=0.75, 1.10, 1.36, 0.46, 0.88, 0.92; P=0.797, 0.372, 0.134, 0.923, 0.636, 0.525).

Analysis of the linear relationships between the 'control' and '+snow' data did expose one significant difference between the two treatments (Figure 4-45 and Table 4-12). With all three variables, there was a significant relationship between the treatments, but for ER in 2003, the relationship was significantly different from 1:1 (as indicated by the slope test); with greater ER in the '+snow' treatment in proportion to the 'control'.

Table 4-12: Test statistics for Heath control vs. +snow regressions.

Variable	Relationship			Y-Intercept		Slope	
	R^2	F	P	t	P	t	P
NEE 2003	0.73	77.27	<0.001	1.75	0.091	-0.62	0.539
ER 2003	0.88	200.76	<0.001	0.50	0.623	2.09	0.047
GPP 2003	0.73	73.16	<0.001	1.25	0.222	-0.25	0.808
NEE 2004	0.44	16.73	<0.001	-0.78	0.447	-0.79	0.440
ER 2004	0.94	187.97	<0.001	0.91	0.378	1.05	0.314
GPP 2004	0.80	51.98	<0.001	0.08	0.936	0.92	0.374

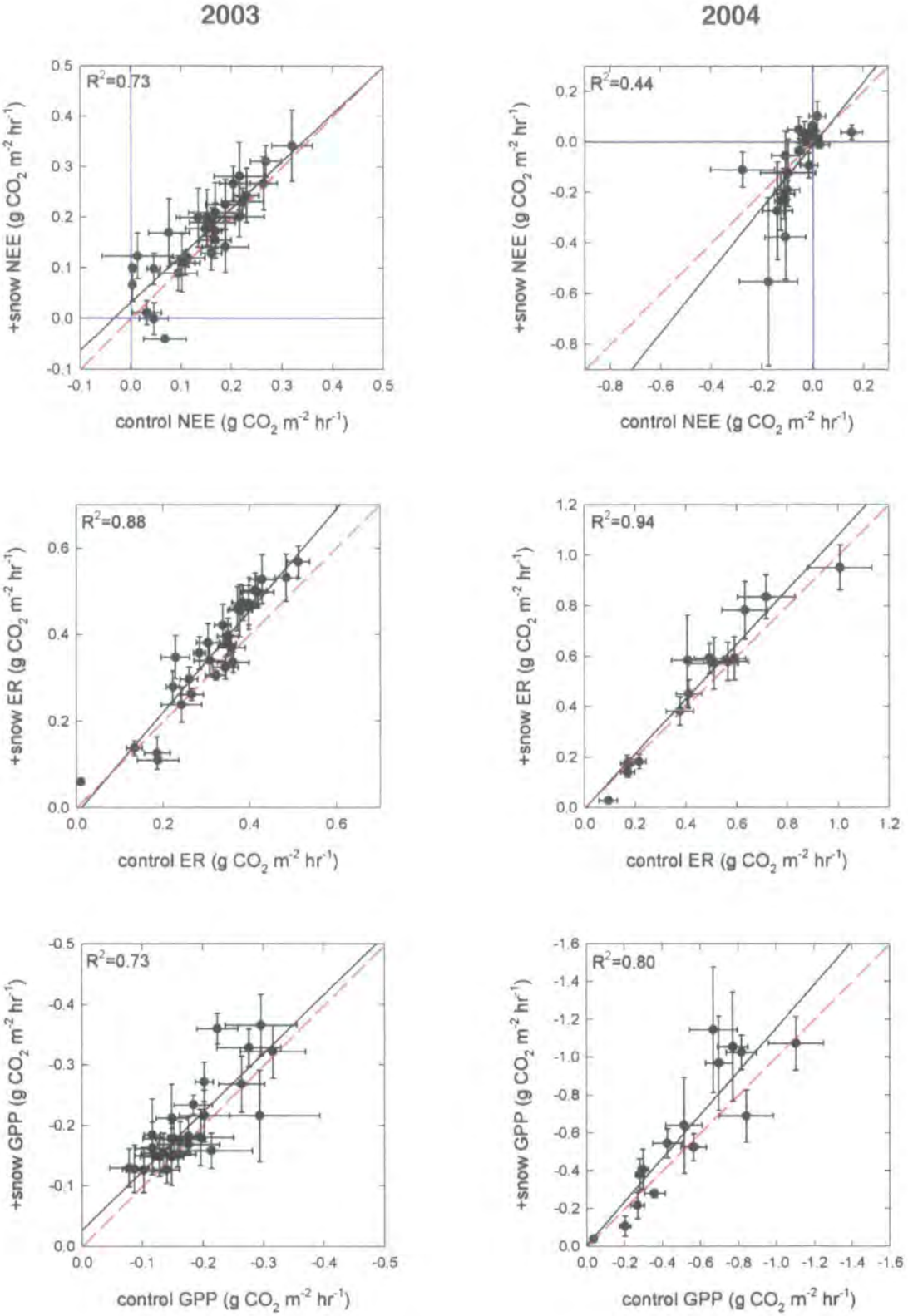

Figure 4-45: Heath 'control' vs. '+snow' treatment mean CO_2 exchange (± standard error; n=5). 2003 data are on the left and 2004 data on the right. The red dashed lines indicate the position of a 1:1 relationship while the black solid lines indicate the line of best fit. The blue solid lines on the NEE graphs indicate the compensation point.

4.4.3 The Ridge

Again, for the Ridge community there was a strong seasonal trend in ER, GPP and NEE, with the greatest fluxes occurring from June through until the end of August each year (see Figure 4-46). Peak ER values were in the region of 0.2 to 0.3 g CO_2 m^{-2} hr^{-1}, while GPP tended to be slightly smaller in magnitude, yet still peaking around -0.2 to -0.3 g CO_2 m^{-2} hr^{-1}. The resulting NEE was typically positive, in the range of approximately 0 to 0.15 g CO_2 m^{-2} hr^{-1}.

Repeated measures ANOVA revealed no significant differences in NEE (F=0.98, 0.20; P=0.356, 0.670; for 2003 and 2004 respectively), ER (F=1.27, 2.11; P=0.293, 0.185) or GPP (F=2.14, 1.24; P=0.182, 0.299) between treatments in either year. The test did, however, reveal significant differences between sample days for

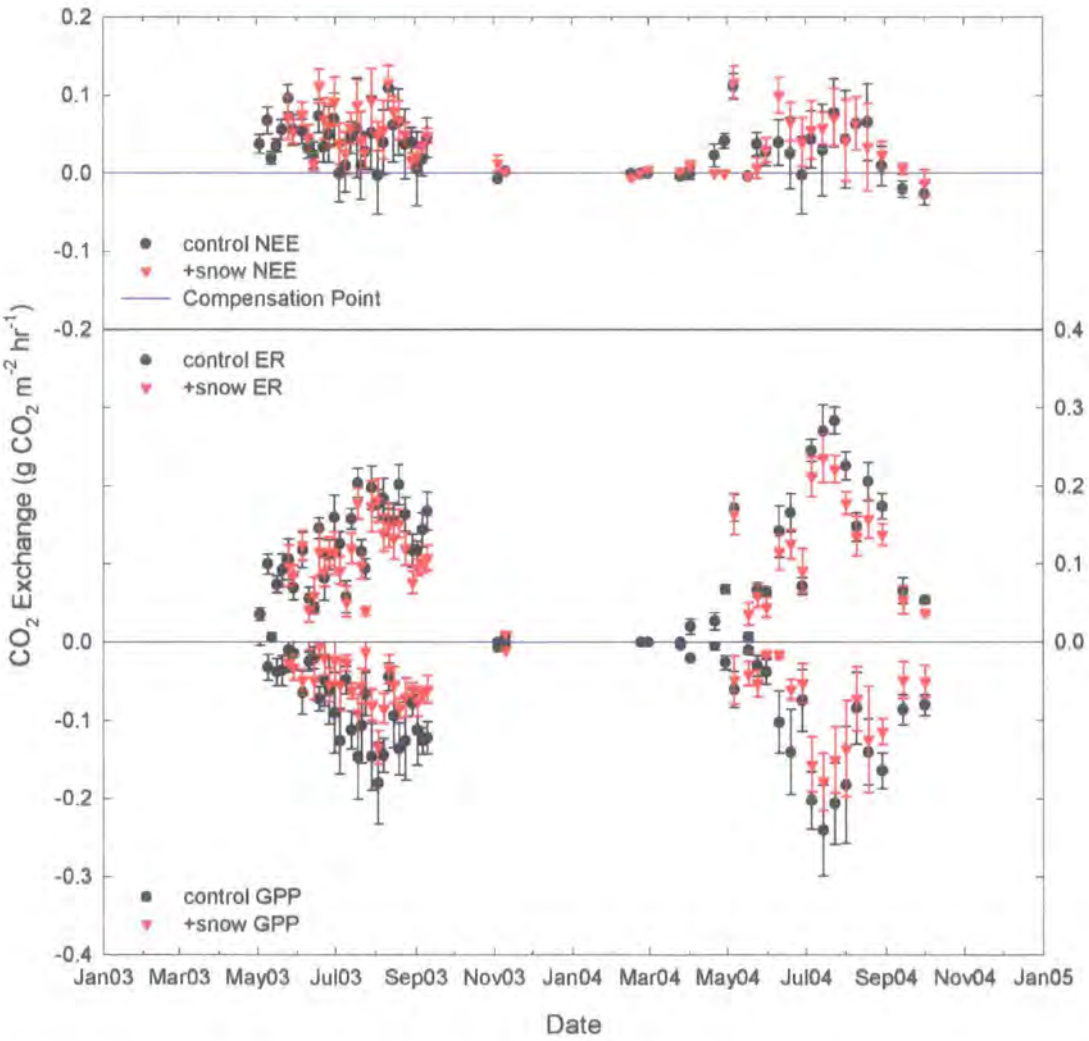

Figure 4-46: Mean study plot CO_2 exchange for the Ridge community (± standard error; n=5).

all three flux variables in both years (F=3.82, 2.23, 13.16, 36.09, 6.09, 6.19; P<0.001, 0.019, <0.001, <0.001, <0.001, <0.001; for NEE03, NEE04, ER03, ER04, GPP03 and GPP04 respectively), but no interaction between sample day and treatment (F=0.68, 0.40, 0.99, 0.86, 0.88, 0.30; P=0.868, 0.953, 0.475, 0.587, 0.630, 0.985).

Analysis of the linear relationships between the 'control' and '+snow' data did expose significant differences between the two treatments (Figure 4-47 and Table 4-13). In each case there was a significant relationship between the treatments, but for ER and GPP, the relationship was significantly different from 1:1 (as indicated by the slope test) in 2003 and 2004, with greater ER and GPP (more negative) in the 'control' treatment in proportion to the '+snow' treatment in both years. In 2003, NEE was also significantly more negative in the 'control' treatment than in the '+snow' treatment (as indicated by the Y-Intercept test).

Table 4-13: Test statistics for Ridge control vs. +snow regressions.

Variable	Relationship			Y-Intercept		Slope	
	R^2	F	P	t	P	t	P
NEE 2003	0.66	49.70	<0.001	3.69	0.001	-1.44	0.162
ER 2003	0.81	103.85	<0.001	1.11	0.278	-3.46	0.002
GPP 2003	0.68	53.71	<0.001	0.76	0.454	-6.63	<0.001
NEE 2004	0.57	28.37	<0.001	1.65	0.115	-1.29	0.212
ER 2004	0.95	294.71	<0.001	1.61	0.130	-5.19	<0.001
GPP 2004	0.80	57.03	<0.001	-0.33	0.750	-3.56	0.003

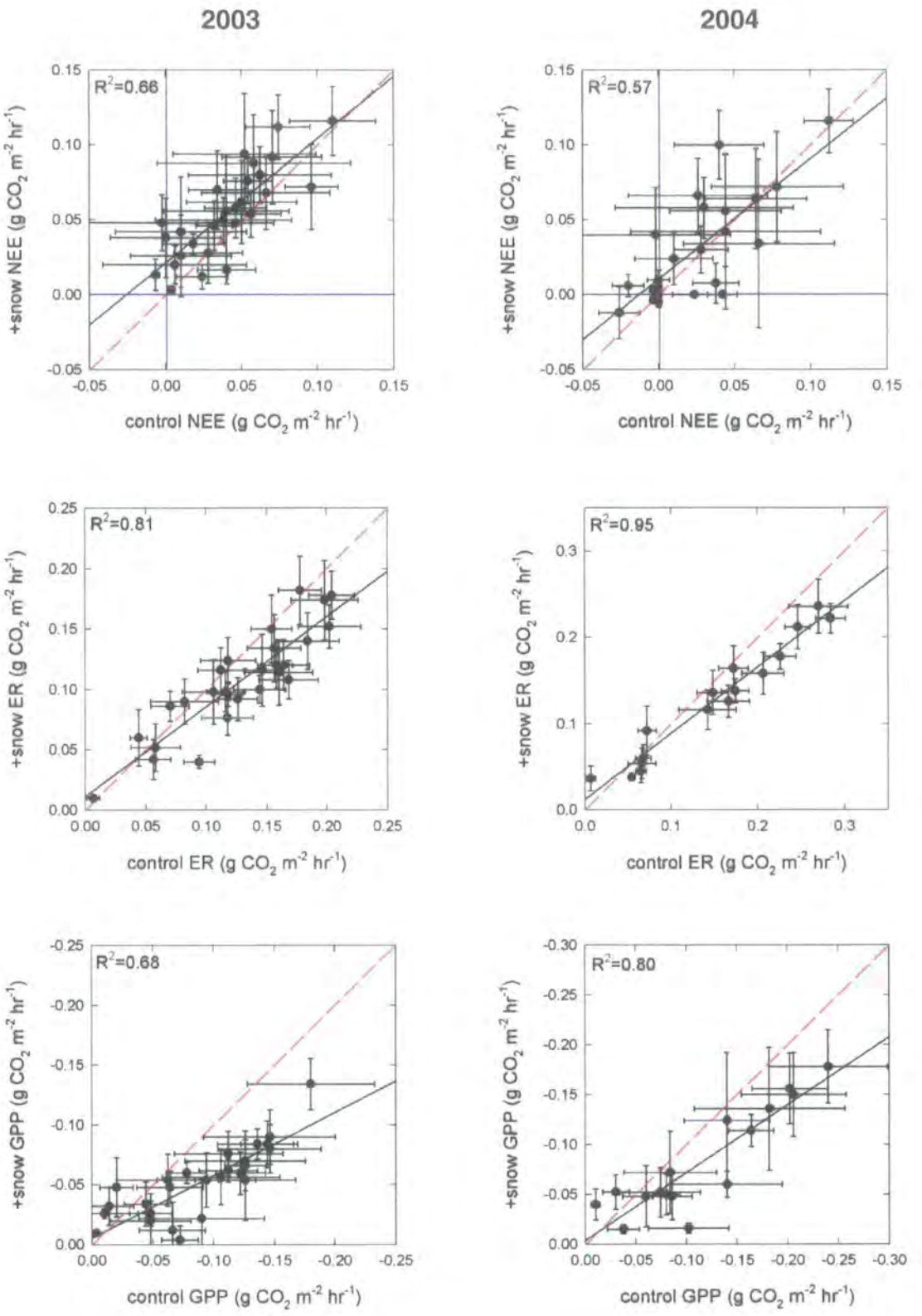

Figure 4-47: Ridge 'control' vs. '+snow' treatment mean CO_2 exchange (± standard error; n=5). 2003 data are on the left and 2004 data on the right. The red dashed lines indicate the position of a 1:1 relationship while the black solid lines indicate the line of best fit. The blue solid lines on the NEE graphs indicate the compensation point.

4.4.4 Community Comparison

When the CO_2 fluxes from the 'control' treatments of the three different communities were compared, all three variables (NEE, ER and GPP) were found to differ significantly between them in both 2003 and 2004. In both years, ER was observed to be significantly greater in the Fen and Heath communities than in the Ridge (F=58.35, 102.24; P<0.001, <0.001; for 2003 and 2004 respectively). The differences in GPP and NEE varied between years. In 2003 for instance, GPP was significantly greater (more negative) in the Fen community than in the Heath or Ridge (F=18.73, P<0.001), whereas in 2004, it was greater in both the Fen and Heath communities than in the Ridge (F=64.40, P<0.001). NEE was significantly more negative in the Fen community than in the Heath in 2003 (F=8.20, P=0.006), while in 2004, it was more negative in the Heath than in the Ridge (F=6.25, P=0.014). The repeated measures ANOVA also revealed significant differences between sample days for each of the three flux variables in both years (F=5.96, 2.44, 32.86, 35.30, 8.93, 19.95; P<0.001, 0.008, <0.001, <0.001, <0.001, <0.001; for NEE03, NEE04, ER03, ER04, GPP03 and GPP04 respectively), as well as significant interaction between sample day and treatment in each case, except with NEE in 2004 (F=2.30, 1.22, 5.89, 4.37, 3.03, 3.83; P<0.001, 0.246, <0.001, <0.001, <0.001, <0.001).

Analysis of the linear relationships between the three communities (Figure 4-48, Figure 4-49 and Table 4-14) revealed significant relationships in every instance for ER and GPP. Significant relationships in NEE were less common. Where the relationships were significant, a number of absolute and proportional differences between the communities were observed. In agreement with the repeated measures ANOVA, ER was found to be greater in the Fen and Heath communities in proportion to the Ridge (as indicated by the slope tests). In 2003 however, ER was also found to be greater, both proportionally and absolutely, in the Fen community than in the Heath. GPP was found to be greater in the Fen community than in the Heath or Ridge in 2003, but in 2004, there was no significant difference between the Fen and Heath, both with proportionally greater GPP than in the Ridge. In the two instances where significant relationships in NEE were observed between the communities, NEE was found to be more negative in the Heath than in the Fen in

2004 (as indicated by the Y-intercept test), and proportionally more positive in the Heath than in the Fen (although less positive at lower values in absolute terms).

Table 4-14: Test statistics for inter-community regressions.

Variable	Relationship			Y-Intercept		Slope	
	R^2	F	P	t	P	t	P
Fen control vs. Heath control							
NEE 2003	0.09	3.26	0.080				
ER 2003	0.80	133.32	<0.001	2.94	0.006	-5.10	<0.001
GPP 2003	0.60	50.39	<0.001	-3.65	0.001	-15.42	<0.001
NEE 2004	0.47	18.79	<0.001	-4.02	0.001	1.80	0.086
ER 2004	0.94	320.25	<0.001	0.49	0.630	0.10	0.924
GPP 2004	0.93	265.73	<0.001	1.55	0.136	1.30	0.209
Fen control vs. Ridge control							
NEE 2003	0.06	2.05	0.162	-		-	-
ER 2003	0.62	51.34	<0.001	1.38	0.179	-18.29	<0.001
GPP 2003	0.47	27.05	<0.001	0.58	0.569	-21.11	<0.001
NEE 2004	0.12	2.74	0.113	-	-	-	-
ER 2004	0.83	98.21	<0.001	1.12	0.276	-21.23	<0.001
GPP 2004	0.74	56.36	<0.001	1.45	0.162	-26.15	<0.001
Heath control vs. Ridge control							
NEE 2003	0.21	8.43	0.006	2.4	0.023	-16.11	<0.001
ER 2003	0.73	85.23	<0.001	0.56	0.582	-13.39	<0.001
GPP 2003	0.29	12.97	0.001	0.53	0.598	-5.74	<0.001
NEE 2004	0.02	0.40	0.535	-		-	-
ER 2004	0.87	138.84	<0.001	1.03	0.317	-25.55	<0.001
GPP 2004	0.78	72.09	<0.001	0.82	0.424	-33.16	<0.001

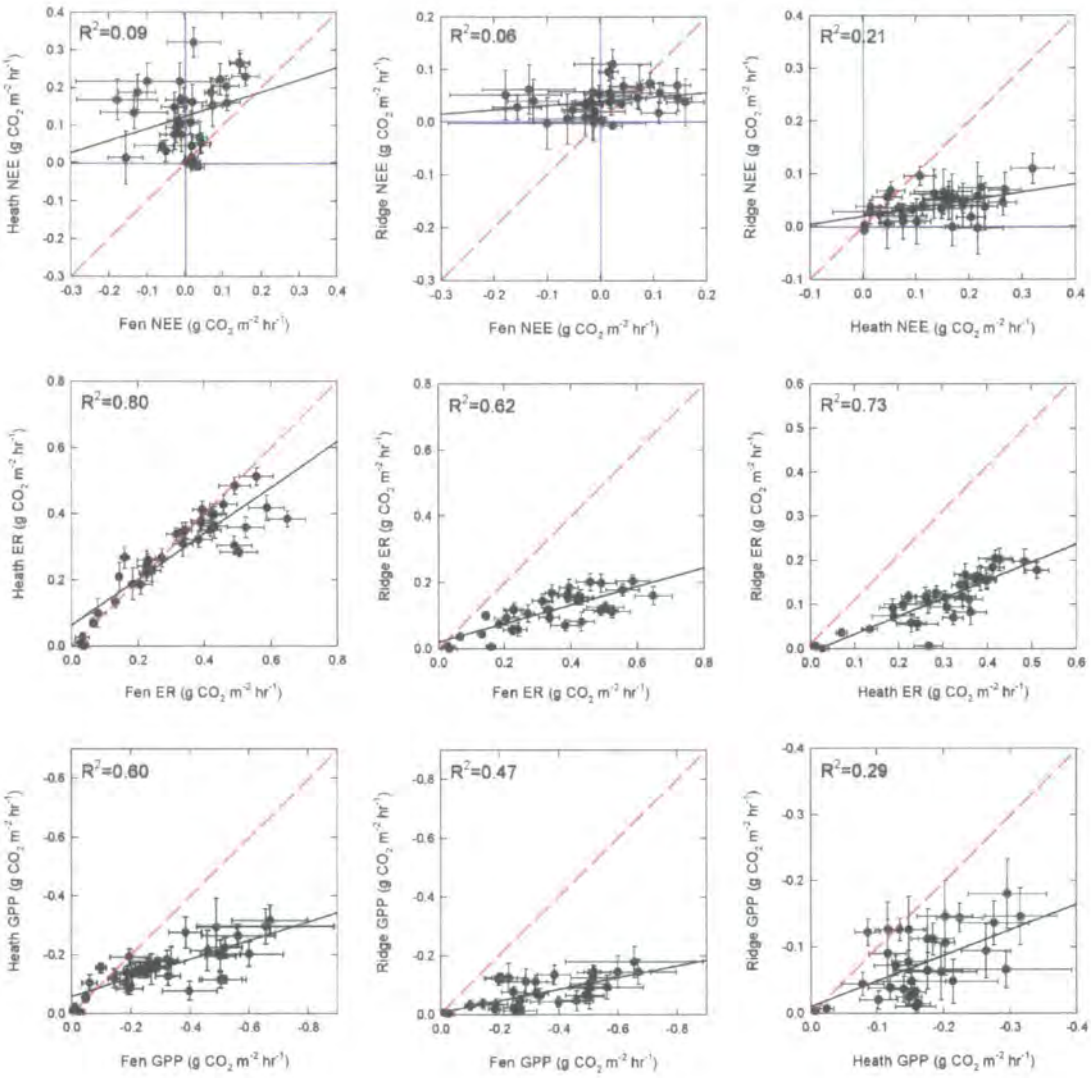

Figure 4-48: 2003 community 'control' vs. community 'control' mean CO_2 exchange (± standard error; n=5). The red dashed lines indicate the position of a 1:1 relationship while the black solid lines indicate the line of best fit. The blue solid lines on the NEE graphs indicate the compensation point.

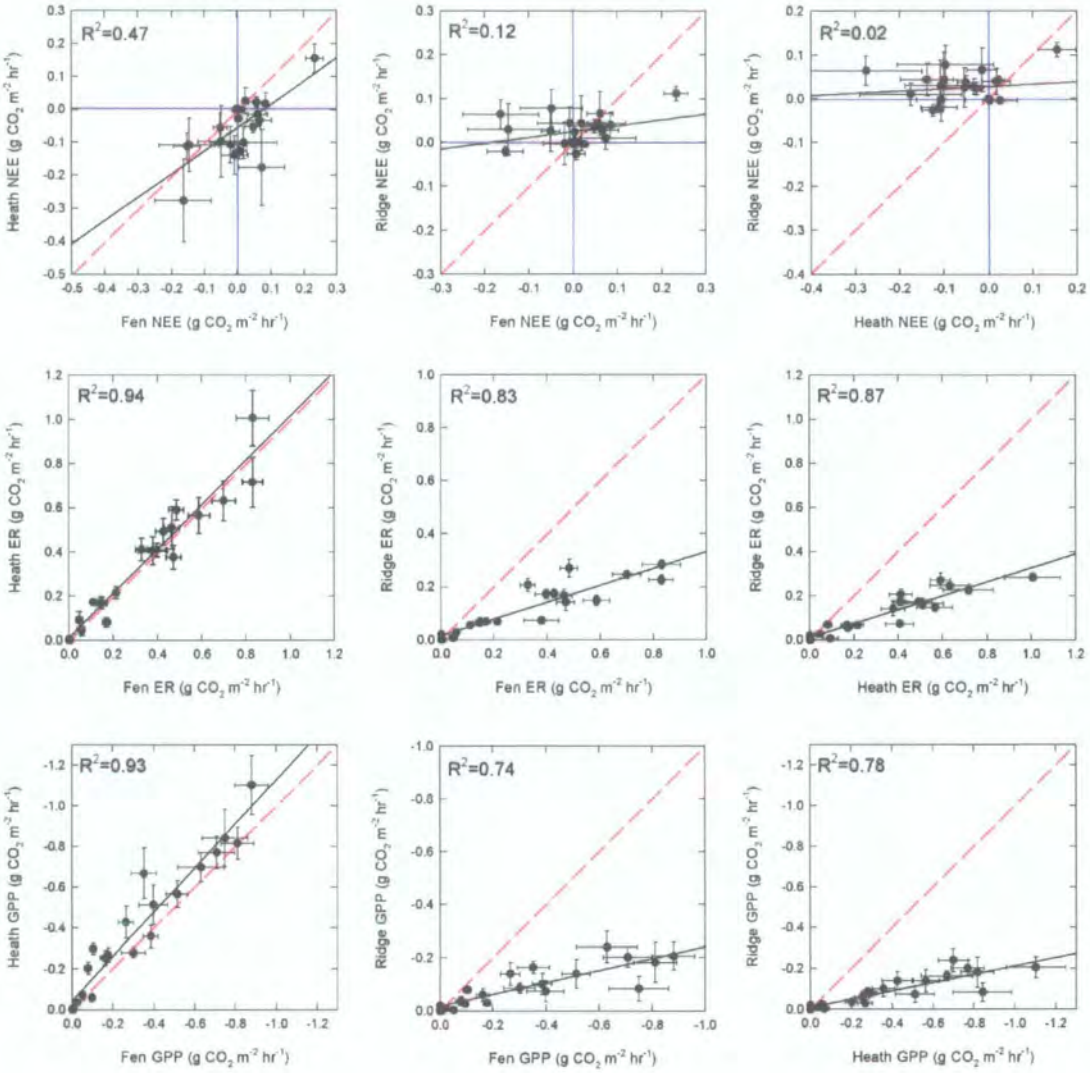

Figure 4-49: 2004 community 'control' vs. community 'control' mean CO_2 exchange (± standard error; n=5). The red dashed lines indicate the position of a 1:1 relationship while the black solid lines indicate the line of best fit. The blue solid lines on the NEE graphs indicate the compensation point.

CHAPTER 5: RESULTS OF THE MONOLITH EXPERIMENT

5.1 ABIOTIC PARAMETERS

5.1.1 Snow Depth and Melt Timing

Both depth and duration of snow cover varied between treatments, as intended (see Figure 5-1). Before the implementation of the February manipulations, the deepest snow cover was found with the '+snow' monoliths (approximately 45 cm). The 'control' and '+melt' monoliths were covered with a slightly shallower pack, while the '0snow' and 'late' monoliths were snow-free. No depths are available for the 'site control' monoliths until later in the spring. Upon manipulation in mid-February, the '+melt' monoliths became snow-free and the 'late' monoliths received a covering of approximately 15 cm. Within a week however, a natural snow melt event occurred, reducing the snow cover on both the 'control' and 'late' monoliths to a thin layer that barely covered the vegetation. By early April the late monoliths were snow-free, followed a week later by the 'control' monoliths and the 'site controls' shortly thereafter. The '+snow' monoliths remained snow covered until the beginning of May.

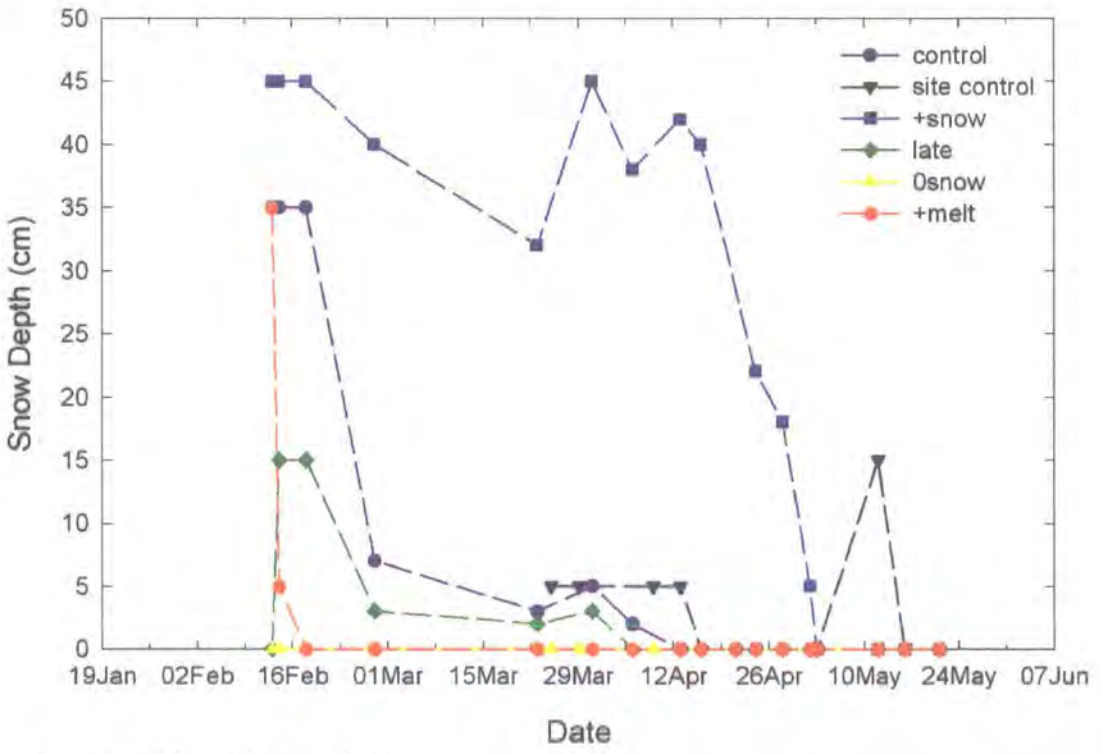

Figure 5-1: Monolith snow depth.

5.1.2 Soil Temperature

A clear seasonal trend in the monthly mean, maximum and minimum monolith soil temperatures was observed for all six treatments, as well as several differences between them (see Figure 5-2, Figure 5-3 and Figure 5-4). The most conspicuous discrepancy occurred from December through until April, when both the mean and minimum temperatures were considerably higher in the '+snow' treatment than any of the others. Furthermore, both the '0snow' and 'late' treatments were cooler (mean and minimum) than the 'controls', '+melts' and 'site controls' during this period. In April, there was a divergence in maximum temperature between treatments, with the '+snow' and 'site control' monoliths remaining cooler than the others. From May onwards, there was little difference between treatments, except for the 'site controls', which remained cooler (mean and maximum) than the research station monoliths all summer.

The results from the manual soil temperature surveys (see Figure 5-5) are congruent with the automatic measurements, showing no significant differences in snow-free season soil temperatures between any of the treatments (F=1.31, P=0.301).

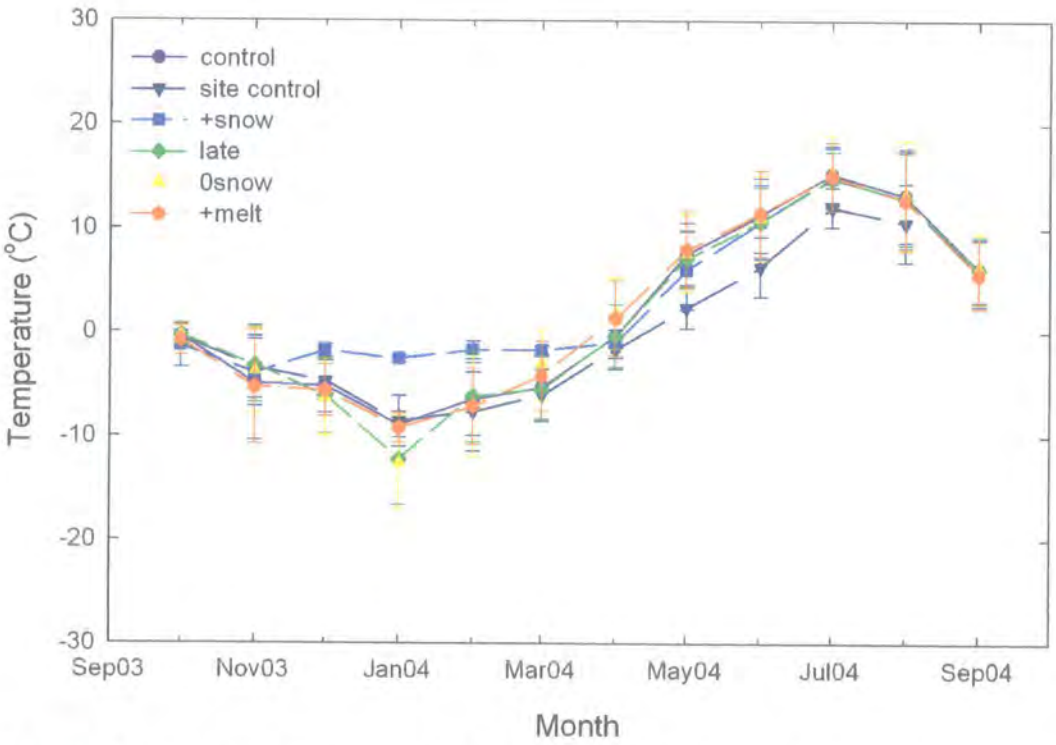

Figure 5-2: Monthly mean monolith soil temperature (± standard error), as measured automatically in one monolith per treatment.

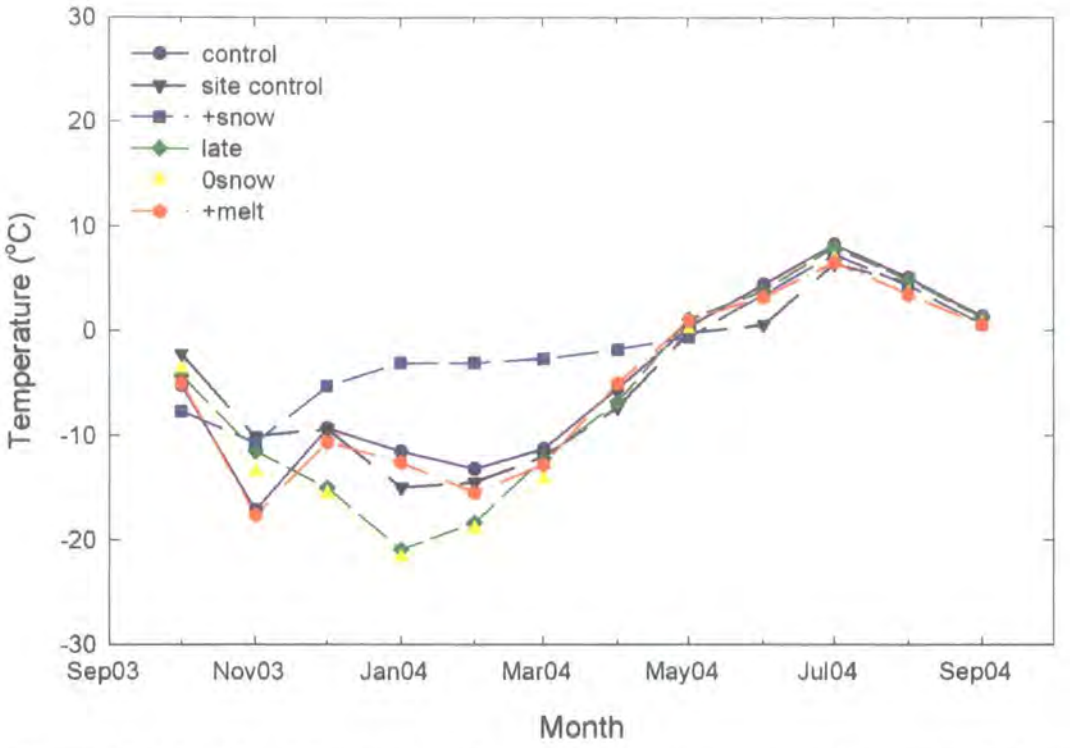

Figure 5-3: Monthly minimum monolith soil temperature, as measured automatically in one monolith per treatment.

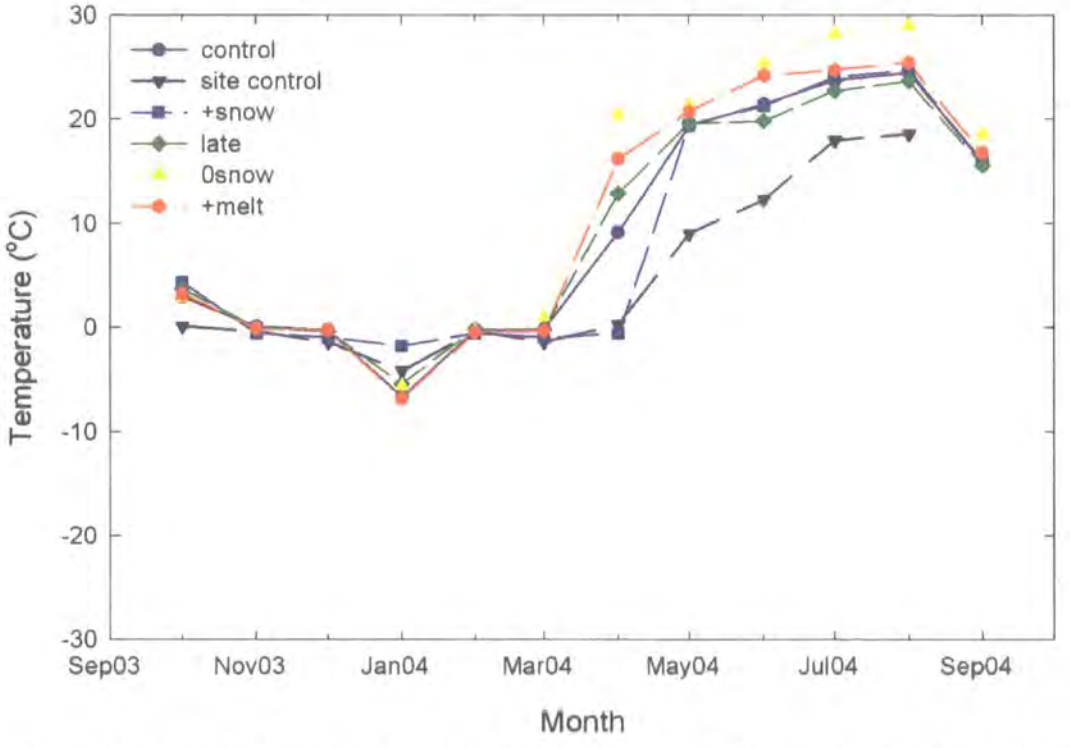

Figure 5-4: Monthly maximum monolith soil temperature, as measured automatically in one monolith per treatment.

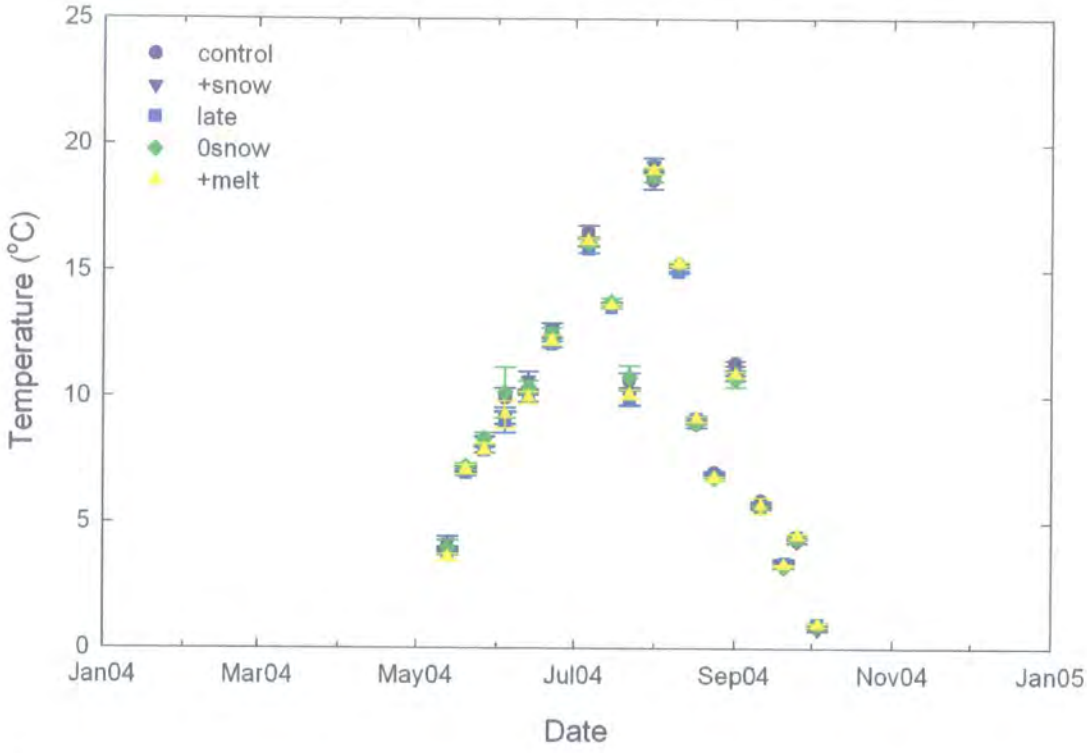

Figure 5-5: Mean monolith soil temperature (± standard error; n=5).

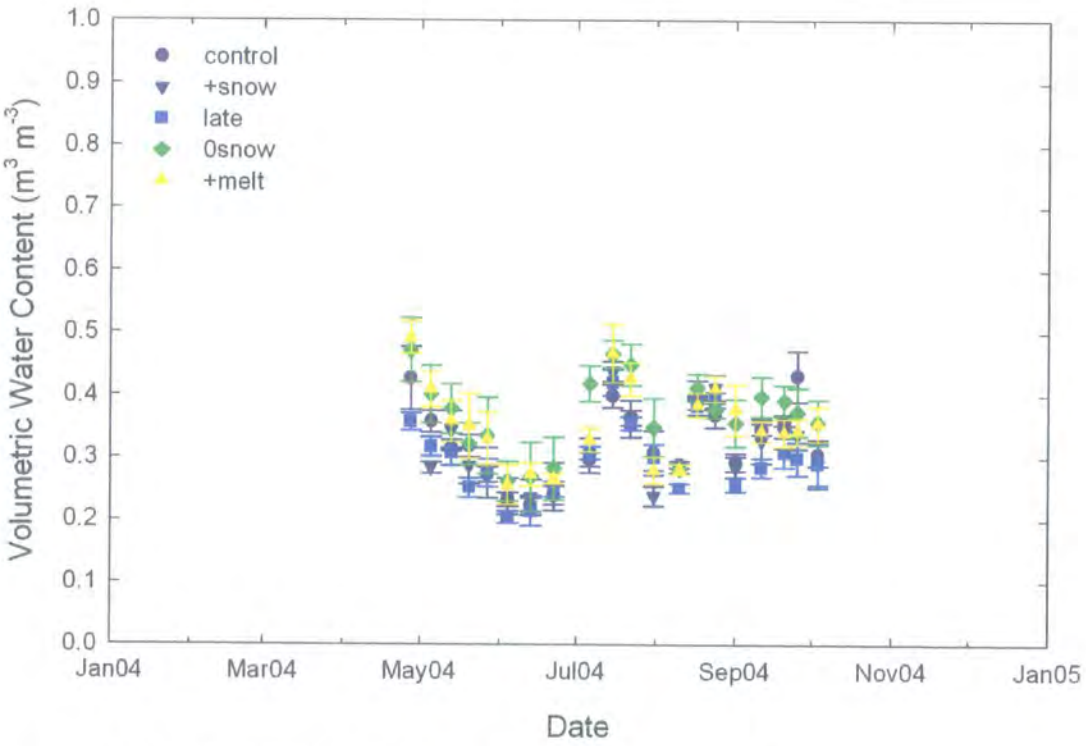

Figure 5-6: Mean monolith soil moisture (± standard error; n=5).

5.1.3 Soil Moisture

There was a moderate level of temporal variability in soil moisture, associated with snow melt at the beginning of the season, and rainfall events thereafter (see Figure 5-6). As with soil temperature however, there were no significant differences in snow-free season soil volumetric water content between any of the treatments (F=2.11, P=0.118).

5.1.4 Air Temperature

Similar to the fieldsite (see section 4.1.5), a clear seasonal trend in air temperature was observed at the research station, with values as low as -28 °C in January at one extreme, to maximum values in excess of 20 °C in August at the other (see Figure 5-7). Again, the winter and spring were characterised by large temperature fluctuations over short time-scales, with switches from freezing to thawing conditions occurring on numerous occasions from February through until late May.

When the annual total GDD accumulation is estimated for each treatment, there is very little difference between them, despite the considerable disparities observed in the timing of snow release. However, comparison of these values with those observed for the fieldsite indicates that annual total GDD accumulation would

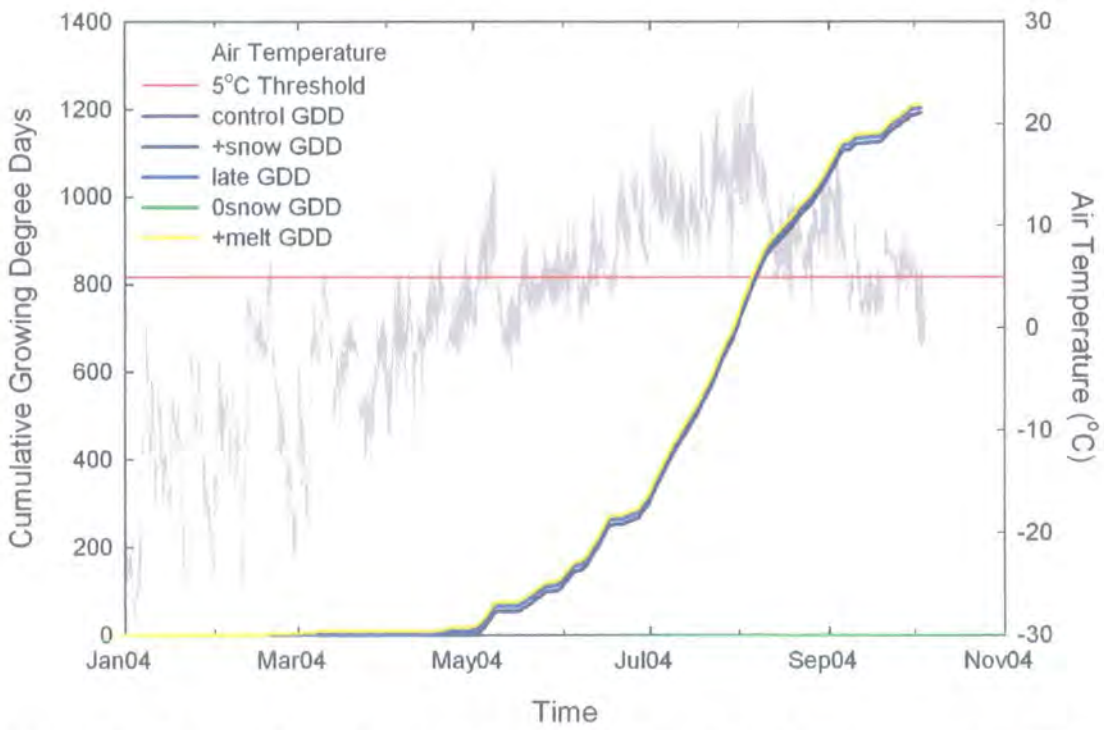

Figure 5-7: Research station hourly air temperature record with annual cumulative GDDs above 5 °C for each treatment.

have been ~17% lower for the 'site control' monoliths than those at the research station.

5.1.5 Solar Radiation

As would be expected, the 2004 incident shortwave radiation record measured at the research station (Figure 5-8) is very similar to the corresponding record for the fieldsite (see section 4.1.6), the seasonal cycle gradually progressing from 24 hour darkness to round the clock daylight, with peak daytime values in the region of 800 W m^{-2}, and back again. When the annual total MJD accumulation is estimated for each treatment, the disparities observed in the timing of snow release do have an effect, the highest MJD accumulations occurring in the '0snow' and '+melt' treatments, with annual totals approximately 15% lower in the 'control' and 'late' treatments and around 25% lower in the '+snow'.

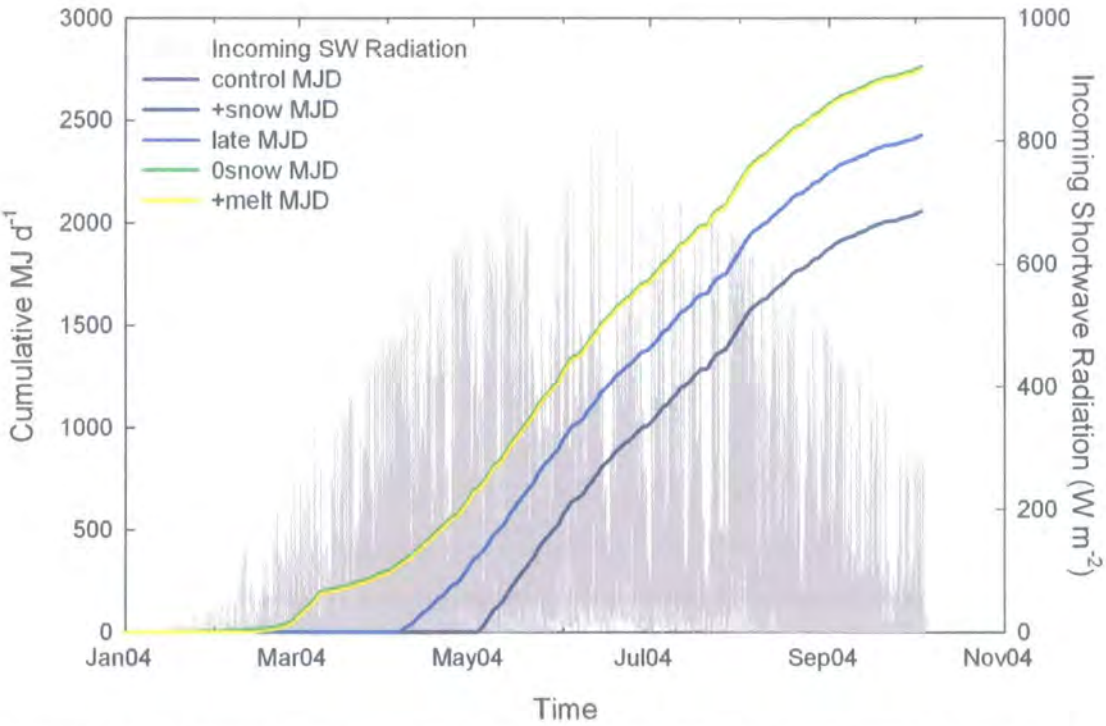

Figure 5-8: Research station hourly incoming shortwave radiation record with annual cumulative MJDs for each treatment.

5.2 PLANT PHENOLOGY

As with the field experiment phenology data (section 4.2), homogeneity resulting from the synchronisation of plant phenology within monoliths of the same treatment prevents the application of the relevant statistical tests in some cases. As before, where this is the case, clear differences between treatments will be assumed to be significant and a '*' will be given in place of *H*, *W*, and *P* values.

5.2.1 Andromeda polifolia

Figure 5-9 displays the mean dates of first occurrence for each of the four phenophases that were monitored for *A. polifolia*. Initial analyses revealed significant differences between treatments in the timing of all of these phases (H=17.36, 20.64, 15.68, 16.86; P=0.004, 0.001, 0.008, 0.005; for flower bud burst, flowering, flower death and fruit production respectively). The results of the pairwise *post hoc* statistical analyses of these data are shown in Table 5-1.

Every observed phenophase occurred later in the 'site control' than in any other treatment, with the two exceptions that there was no significant difference between the 'site control' and the '+snow treatment' for the first phenophase, flower bud burst, and there was not quite a significant difference between the 'site control' and the '0snow' treatment with flowering. By the last observed phenophase, fruit production, the 'site control' was over five weeks later than the other treatments.

Flower bud burst occurred significantly earlier in the '+melt' treatment than in any other, but with each subsequent phenophase, the number of treatments with which the '+melt' significantly differed, became smaller and smaller. The '+melt'

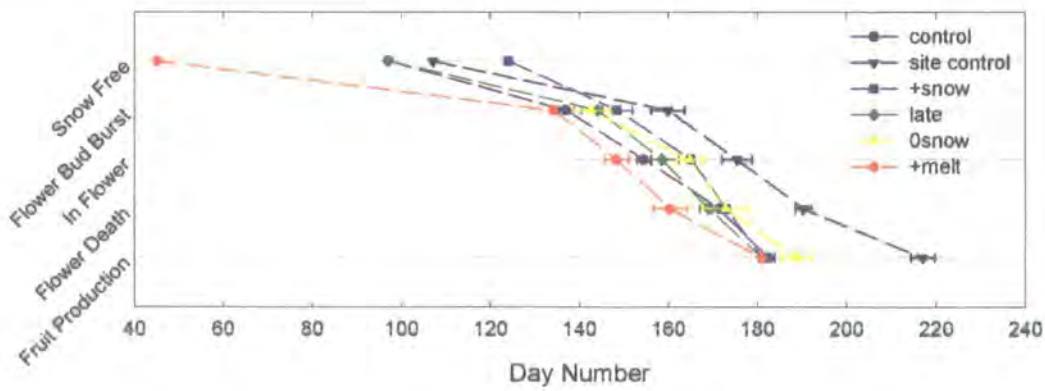

Figure 5-9: Mean dates of phenophase first occurrence for *A. polifolia* (± standard error).

treatment only differed significantly from the 'control' for flower bud burst (several days).

For the first two observed phenophases, the '+snow' treatment was significantly later than the 'control', by one to two weeks in each case. The '0snow' treatment was also significantly later (around one week) than the control, but only for the second phenophase, flowering.

Table 5-1: Results of *post hoc* statistical analyses of *A. polifolia* phenology data.

Phenophase	Comparison	Difference	*W*	*P*
Flower Bud Burst	control vs. site control	– +	15.0	0.012
	control vs. +snow	– +	17.0	0.029
	control vs. late	0	20.5	0.148
	control vs. 0snow	0	23.0	0.366
	control vs. +melt	+ –	*	*
	site control vs. +snow	0	36.0	0.091
	site control vs. late	+ –	38.0	0.035
	site control vs. 0snow	+ –	38.0	0.035
	site control vs. +melt	+ –	*	*
	+snow vs. late	0	31.5	0.443
	+snow vs. 0snow	0	32.5	0.332
	+snow vs. +melt	+ –	*	*
	late vs. 0snow	0	29.0	0.829
	late vs. +melt	+ –	*	*
	0snow vs. +melt	+ –	*	*
In Flower	control vs. site control	– +	15.0	0.009
	control vs. +snow	– +	*	*
	control vs. late	0	21.5	0.416
	control vs. 0snow	– +	17.0	0.043
	control vs. +melt	0	31.0	0.132
	site control vs. +snow	+ –	*	*
	site control vs. late	+ –	35.0	0.018
	site control vs. 0snow	0	33.0	0.063
	site control vs. +melt	+ –	35.0	0.018
	+snow vs. late	+ –	*	*
	+snow vs. 0snow	0	*	*
	+snow vs. +melt	+ –	*	*
	late vs. 0snow	0	14.5	0.353
	late vs. +melt	0	23.5	0.134
	0snow vs. +melt	+ –	25.5	0.040
Flower Death	control vs. site control	– +	15.0	0.008
	control vs. +snow	0	*	*
	control vs. late	0	28.0	0.456
	control vs. 0snow	0	24.5	0.584

	control vs. +melt	0	32.0	0.075
	site control vs. +snow	+ –	*	*
	site control vs. late	+ –	35.0	0.014
	site control vs. 0snow	+ –	40.0	0.009
	site control vs. +melt	+ –	35.0	0.013
	+snow vs. late	+ –	*	*
	+snow vs. 0snow	0	*	*
	+snow vs. +melt	+ –	*	*
	late vs. 0snow	0	17.0	0.524
	late vs. +melt	0	23.0	0.169
	0snow vs. +melt	0	31.5	0.118
Fruit Production	control vs. site control	– +	15.0	0.013
	control vs. +snow	0	*	*
	control vs. late	0	*	*
	control vs. 0snow	0	18.5	0.228
	control vs. +melt	0	*	*
	site control vs. +snow	+ –	*	*
	site control vs. late	+ –	*	*
	site control vs. 0snow	+ –	22.0	0.044
	site control vs. +melt	+ –	*	*
	+snow vs. late	0	*	*
	+snow vs. 0snow	+ –	*	*
	+snow vs. +melt	0	*	*
	late vs. 0snow	0	*	*
	late vs. +melt	0	*	*
	0snow vs. +melt	0	*	*

5.2.2 Betula nana

Figure 5-10 displays the mean dates of first occurrence for each of the six phenophases that were monitored for *B. nana*. Initial analyses only revealed significant differences between treatments in the timing of the first two of these phases (H=19.43, 19.28, 8.82, 3.27, 4.21, 4.9; P=0.002, 0.002, 0.117, 0.659, 0.52, 0.428; for leaf bud burst, full leaf opening, flowering and the three stages of leaf senescence respectively). The results of the pairwise *post hoc* statistical analyses of these data are shown in Table 5-2.

Both leaf bud burst and full leaf opening occurred significantly later in the 'site control' than in any other treatment, with the exception of the '+snow' treatment, and in the case of leaf bud burst, the '+melt' treatment as well.

The '+snow' treatment was also significantly later than the 'control' and 'late' treatments for these two phenophases (around one week in each case). In addition, leaf bud burst occurred significantly later in the '+snow' treatment than

in the '0snow' and full leaf opening occurred significantly later than in the '+melt' (around one and two weeks respectively).

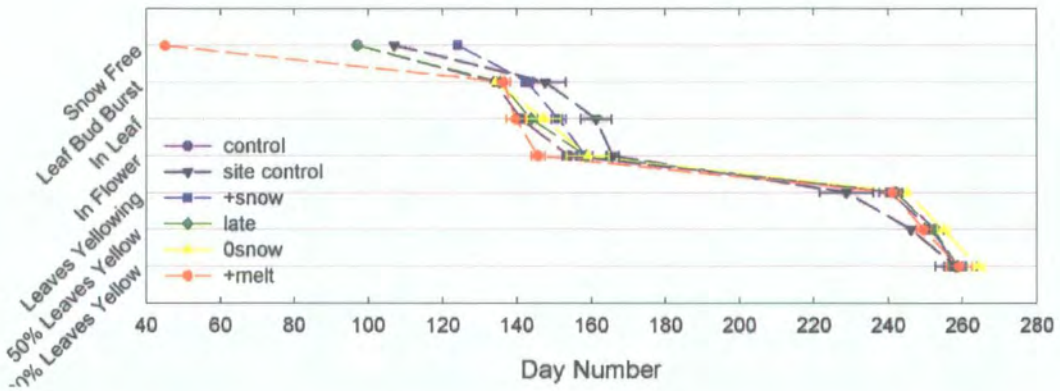

Figure 5-10: Mean dates of phenophase first occurrence for *B. nana* (± standard error).

Table 5-2: Results of *post hoc* statistical analyses of *B. nana* phenology data.

Phenophase	Comparison	Difference	*W*	*P*
Leaf Bud Burst	control vs. site control	– +	*	*
	control vs. +snow	– +	*	*
	control vs. late	0	*	*
	control vs. 0snow	0	*	*
	control vs. +melt	0	*	*
	site control vs. +snow	0	26.0	0.900
	site control vs. late	+ –	38.0	0.030
	site control vs. 0snow	+ –	*	*
	site control vs. +melt	0	28.0	0.129
	+snow vs. late	+ –	28.5	0.032
	+snow vs. 0snow	+ –	*	*
	+snow vs. +melt	0	20.5	0.115
	late vs. 0snow	0	*	*
	late vs. +melt	0	21.5	0.844
	0snow vs. +melt	0	*	*
In Leaf	control vs. site control	– +	*	*
	control vs. +snow	– +	*	*
	control vs. late	– +	*	*
	control vs. 0snow	– +	*	*
	control vs. +melt	0	*	*
	site control vs. +snow	0	36.0	0.085
	site control vs. late	+ –	40.0	0.010
	site control vs. 0snow	+ –	38.0	0.032
	site control vs. +melt	+ –	40.0	0.010
	+snow vs. late	+ –	37.0	0.041
	+snow vs. 0snow	0	33.5	0.228
	+snow vs. +melt	+ –	38.5	0.022
	late vs. 0snow	0	26.5	0.905
	late vs. +melt	0	33.0	0.257
	0snow vs. +melt	0	33.5	0.217

5.2.3 Empetrum hermaphroditum

Figure 5-11 displays the mean dates of first occurrence for each of the six phenophases that were monitored for *E. hermaphroditum*. Initial analyses only revealed a significant difference between treatments in the timing of the second of these phases, flower death (H=8.64, 15, 9.58, 10.29; P=0.071, 0.005, 0.088, 0.067; for flowering, flower death, fruit production and fruit ripening respectively). Unfortunately, no pairwise *post hoc* analyses are possible, as there was no variance within any of the treatments. Nevertheless, the significant difference between treatments appears to have resulted from flower death occurring several days later in

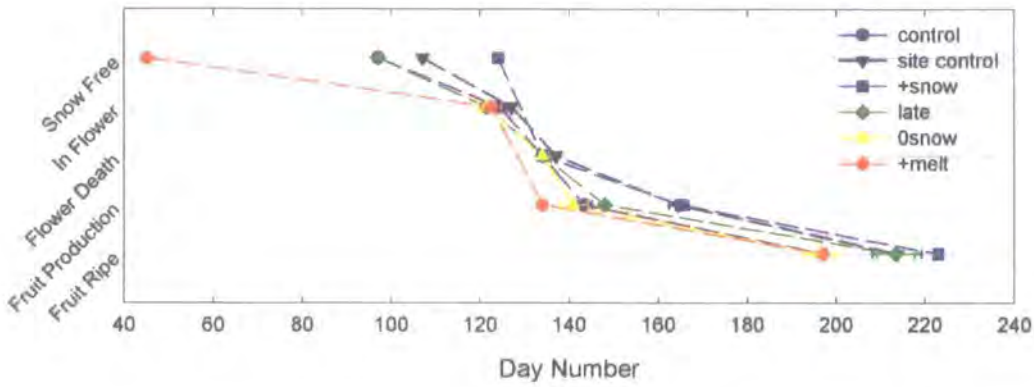

Figure 5-11: Mean dates of phenophase first occurrence for *E. hermaphroditum* (± standard error).

the 'site control' treatment than any of the others. There do appear to be differences between treatments for the other phenophases (as indicated by the near significant *P* values). However, due to the infrequency of their occurrence, it is likely that the sample sizes were too small to prove the significance of any discrepancies statistically.

5.2.4 Vaccinium uliginosum

Figure 5-12 displays the mean dates of first occurrence for each of the nine phenophases that were monitored for *V. uliginosum*. Initial analyses revealed significant differences between treatments for the first five of these phases (with the exception of the very first stage; flower buds), but not the last four (H=8.52, 16.57, 17.12, 16.21, 13.12, 8.58, 5.76, 7.01, 4.66; P=0.130, 0.005, 0.004, 0.006, 0.022, 0.127, 0.218, 0.220, 0.459; for the appearance of flower buds, leaf bud burst, full leaf opening, flower bud burst, flowering, flower death and the three stages of leaf senescence respectively). The results of the pairwise *post hoc* statistical analyses of these data are shown in Table 5-3.

All four of the phenophases that differed significantly between treatments occurred significantly (or at least very nearly significantly) later in the 'site control' than in any other treatment. In each case, the differences were in the region of two weeks.

With the exception of the '+melt' treatment, leaf bud burst occurred significantly earlier in the control treatment than in any other (several days to a week). The occurrence of full leaf opening however, was only significantly earlier

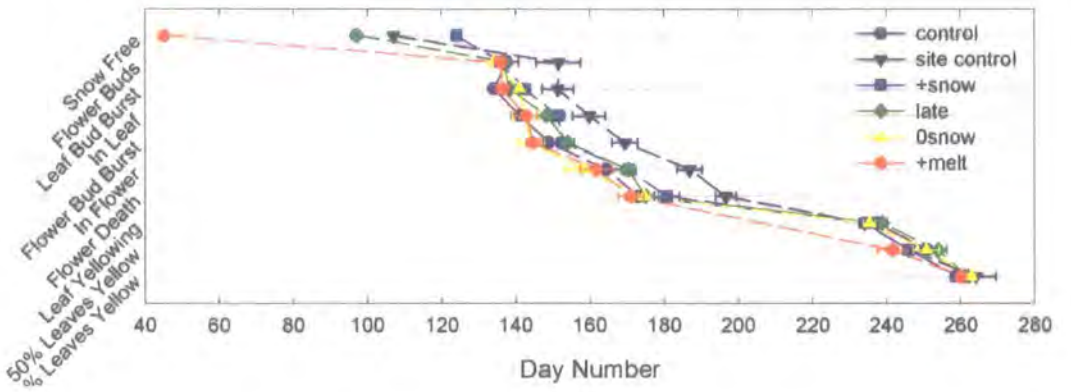

Figure 5-12: Mean dates of phenophase first occurrence for *V. uliginosum* (± standard error).

in the 'control' treatment when compared with the '+snow' and the 'site control' (around one week and two weeks respectively). For the remaining phenophases, the only treatment to differ from the 'control' was the 'site control', although, as mentioned above, these differences were not quite significant.

There were also some significant, if inconsistent, differences associated with the '+melt' treatment. As well as the differences with the 'site control' mentioned above, leaf bud burst occurred earlier in the '+melt' than in the '0snow' treatment. Flower bud burst on the other hand, occurred earlier in the '+melt' than in the '+snow' or 'late' treatments.

Table 5-3: Results of *post hoc* statistical analyses of *V. uliginosum* phenology data.

Phenophase	Comparison	Difference	*W*	*P*
Leaf Bud Burst	control vs. site control	− +	*	*
	control vs. +snow	− +	*	*
	control vs. late	− +	*	*
	control vs. 0snow	− +	*	*
	control vs. +melt	0	*	*
	site control vs. +snow	0	20.0	0.057
	site control vs. late	+ −	21.0	0.031
	site control vs. 0snow	+ −	*	*
	site control vs. +melt	0	15.0	0.077
	+snow vs. late	0	34.0	0.121
	+snow vs. 0snow	0	*	*
	+snow vs. +melt	0	28.0	0.085
	late vs. 0snow	0	*	*
	late vs. +melt	0	24.5	0.608
	0snow vs. +melt	+ −	*	*

In Leaf	control vs. site control	– +	15.0	0.011
	control vs. +snow	– +	16.5	0.021
	control vs. late	0	19.0	0.075
	control vs. 0snow	0	22.5	0.740
	control vs. +melt	0	23.0	0.695
	site control vs. +snow	0	36.0	0.088
	site control vs. late	+ –	38.0	0.033
	site control vs. 0snow	+ –	40.0	0.010
	site control vs. +melt	+ –	35.0	0.018
	+snow vs. late	0	31.5	0.403
	+snow vs. 0snow	0	35.5	0.075
	+snow vs. +melt	0	32.0	0.080
	late vs. 0snow	0	32.5	0.288
	late vs. +melt	0	29.5	0.281
	0snow vs. +melt	0	25.0	1.000
Flower Bud Burst	control vs. site control	0	12.0	0.060
	control vs. +snow	0	16.0	0.373
	control vs. late	0	14.5	0.369
	control vs. 0snow	0	22.5	0.607
	control vs. +melt	0	19.0	0.874
	site control vs. +snow	+ –	40.0	0.010
	site control vs. late	+ –	35.0	0.016
	site control vs. 0snow	+ –	40.0	0.011
	site control vs. +melt	+ –	35.0	0.017
	+snow vs. late	0	23.5	0.766
	+snow vs. 0snow	0	35.5	0.100
	+snow vs. +melt	+ –	33.0	0.050
	late vs. 0snow	0	27.0	0.093
	late vs. +melt	+ –	25.0	0.047
	0snow vs. +melt	0	24.0	0.896
In Flower	control vs. site control	0	7.0	0.065
	control vs. +snow	0	9.0	0.653
	control vs. late	0	9.0	0.653
	control vs. 0snow	0	14.0	0.559
	control vs. +melt	0	11.0	1.000
	site control vs. +snow	+ –	30.0	0.031
	site control vs. late	+ –	30.0	0.031
	site control vs. 0snow	+ –	35.0	0.018
	site control vs. +melt	+ –	30.0	0.031
	+snow vs. late	0	10.5	1.000
	+snow vs. 0snow	0	16.0	0.195
	+snow vs. +melt	0	13.0	0.346
	late vs. 0snow	0	16.0	0.195
	late vs. +melt	0	13.0	0.346
	0snow vs. +melt	0	14.5	0.693

5.3 MONOLITH CARBON DIOXIDE EXCHANGE

As with the field experiment, in all treatments there was a clear seasonal trend in ER and GPP, both increasing in magnitude as the snow-free season progressed, reaching peak values of approximately 0.7 to 1.0 g CO_2 m^{-2} hr^{-1} and -0.6 to -1.1 g CO_2 m^{-2} hr^{-1} (for ER and GPP respectively) in mid to late July, decreasing markedly in August and more gradually thereafter (see Figure 5-13). By the end of the study period in October, both ER and GPP values were approaching zero. The resulting NEE did not exhibit such a distinct seasonal trend. As ER exceeded GPP at the beginning of the study period, the initial net CO_2 flux was positive, but became smaller as GPP values increased in relation to ER. In some treatments, there was a switch to net CO_2

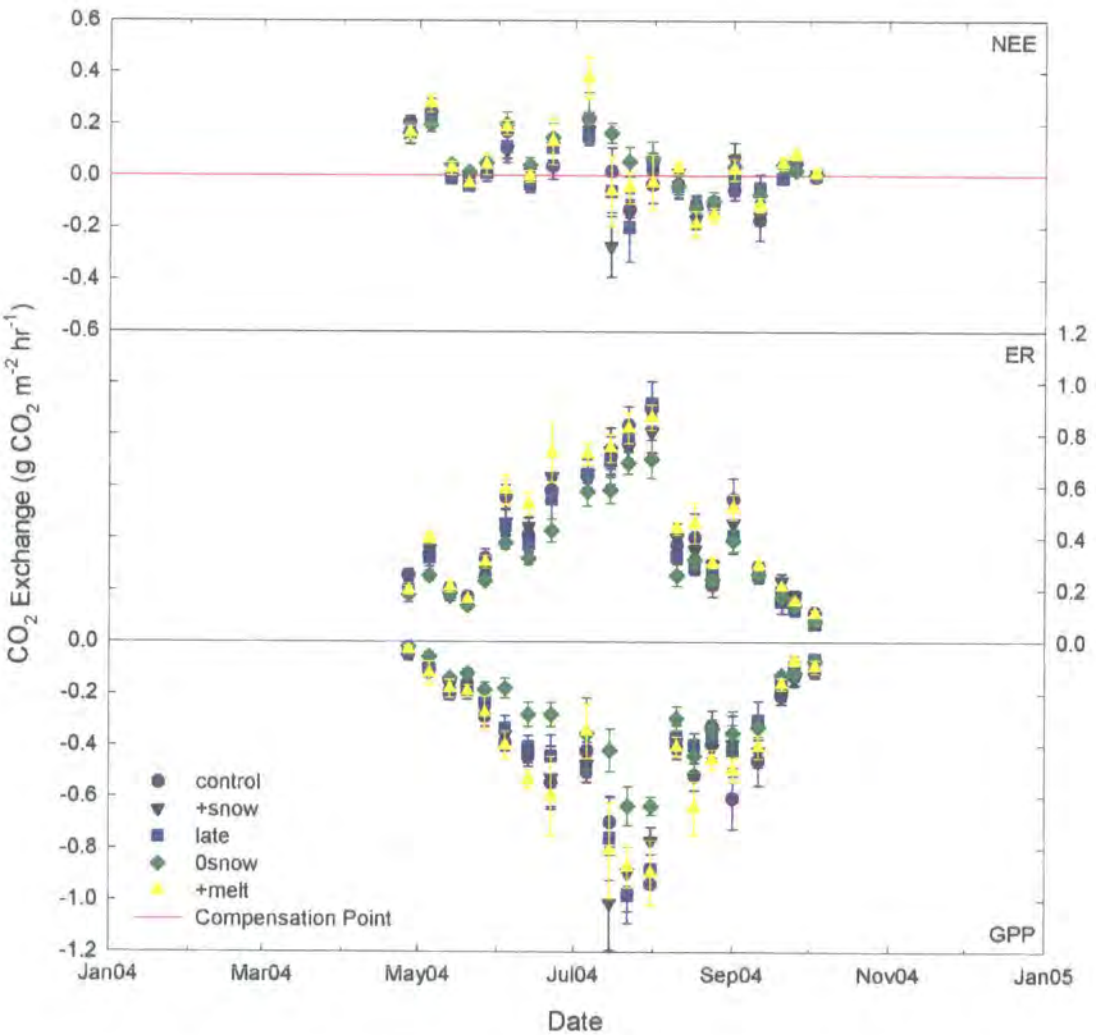

Figure 5-13: Mean monolith CO_2 exchange (± standard error; n=5).

assimilation around mid-July. Overall, NEE values were rarely far from zero, ranging between 0.5 and -0.4 g CO_2 m^{-2} hr^{-1} in the most extreme cases.

Repeated measures ANOVA revealed significant/nearly significant differences between treatments for ER (F=4.37, P=0.011) and GPP (F=2.78, P=0.055), but not NEE (F=1.35, P=0.288). It also revealed significant differences between sampling days for all three flux variables (F=30.62, 164.51, 81.13; P<0.001, <0.001, <0.001; for NEE, ER and GPP respectively) and a significant interaction between sample day and treatment for NEE (F=1.56, P=0.005) and GPP (F=1.44, P=0.017), but not ER (F=1.07, P=0.339).

Table 5-4 shows the results of the pairwise *post hoc* analyses used to identify which treatments differed. ER was significantly lower in the '0snow' treatment than in either the 'control' or the '+melt'. Similarly, GPP was significantly lower (more positive) in the '0snow' treatment than in the 'control', '+melt' or '+snow'.

Table 5-4: Test statistics for pairwise *post hoc* analyses of the study period mean monolith CO_2 exchange.

Variable	Comparison	*t*	*P*
ER	control vs. +snow	0.14	0.677
	control vs. late	1.66	0.140
	control vs. 0snow	**3.77**	**0.007**
	control vs. +melt	-1.02	0.345
	+snow vs. late	0.83	0.432
	+snow vs. 0snow	2.30	0.061
	+snow vs. +melt	-1.19	0.271
	late vs. 0snow	1.79	0.117
	late vs. +melt	-2.27	0.057
	0snow vs. +melt	**-3.90**	**0.006**
GPP	control vs. +snow	-0.21	0.843
	control vs. late	-0.78	0.464
	control vs. 0snow	**-3.08**	**0.018**
	control vs. +melt	0.04	0.968
	+snow vs. late	-0.60	0.567
	+snow vs. 0snow	**-2.98**	**0.020**
	+snow vs. +melt	0.22	0.833
	late vs. 0snow	-2.24	0.060
	late vs. +melt	0.72	0.498
	0snow vs. +melt	**2.64**	**0.038**

Analysis of the linear relationships between the different treatments (Figure 5-14, Figure 5-15, Figure 5-16 and Table 5-5) revealed significant differences between treatments in all three variables. ER was found to be proportionally lower in the '0snow' treatment than in the 'control', '+snow', 'late' or '+melt' (as indicated by the slope tests). ER was also proportionally lower in the '+snow' treatment than in the '+melt'. The Y-intercept tests also indicate two absolute differences, with lower ER in the late treatment than in either the '+snow' or '+melt'. Similar to ER, GPP was found to be proportionally lower in the '0snow' treatment than in the 'control', '+snow', 'late' or '+melt'. NEE was found to be proportionally greater, in both directions, in the 'control' and '+snow' treatments than in either the 'late' or '0snow'. It was also found to be more positive in the '0snow' treatment than in the 'late', although this result is largely due to the influence of two spurious outliers.

Table 5-5: Test statistics for the pairwise inter-treatment regressions.

Variable	Relationship			Y-Intercept		Slope	
	R^2	F	P	t	P	t	P
control vs. +snow							
NEE	0.56	22.08	<0.001	0.19	0.852	-0.88	0.392
ER	0.95	335.91	<0.001	1.15	0.265	-1.97	0.065
GPP	0.84	92.45	<0.001	0.45	0.659	0.76	0.459
control vs. late							
NEE	0.80	73.80	<0.001	0.32	0.754	-2.42	0.026
ER	0.96	468.47	<0.001	1.88	0.077	-0.08	0.939
GPP	0.93	257.61	<0.001	0.72	0.479	-0.64	0.531
control vs. 0snow							
NEE	0.70	42.79	<0.001	3.71	0.002	-2.62	0.017
ER	0.97	501.18	<0.001	0.20	0.847	-6.20	<0.001
GPP	0.92	199.54	<0.001	0.68	0.508	-7.91	<0.001
control vs. +melt							
NEE	0.82	84.29	<0.001	1.81	0.087	0.59	0.565
ER	0.95	343.88	<0.001	0.70	0.491	0.34	0.741
GPP	0.93	241.73	<0.001	0.36	0.726	0.37	0.714
+snow vs. late							
NEE	0.72	43.59	<0.001	0.01	0.994	-3.28	0.004
ER	0.97	518.81	<0.001	-2.72	0.015	1.63	0.121
GPP	0.90	161.64	<0.001	0.13	0.894	0.75	0.464
+snow vs. 0snow							
NEE	0.30	7.14	0.016	2.61	0.018	-3.49	0.003
ER	0.95	320.45	<0.001	-0.30	0.771	-3.52	0.003
GPP	0.79	64.68	<0.001	1.28	0.219	-5.69	<0.001
+snow vs. +melt							
NEE	0.71	41.91	<0.001	1.88	0.078	-0.43	0.670
ER	0.98	757.24	<0.001	0.18	0.860	2.49	0.023
GPP	0.90	150.33	<0.001	-0.90	0.379	-0.69	0.500
late vs. 0snow							
NEE	0.54	21.12	<0.001	3.29	0.004	-1.80	0.088
ER	0.98	737.16	<0.001	3.13	0.006	-7.85	<0.001
GPP	0.89	147.82	<0.001	-1.71	0.105	-6.99	<0.001
late vs. +melt							
NEE	0.75	54.04	<0.001	1.91	0.072	1.01	0.297
ER	0.94	273.27	<0.001	2.63	0.017	-0.06	0.956
GPP	0.90	154.62	<0.001	1.47	0.159	-0.48	0.640
0snow vs. +melt							
NEE	0.69	39.70	<0.001	1.26	0.226	0.81	0.429
ER	0.93	239.58	<0.001	0.85	0.407	3.23	0.005
GPP	0.88	132.49	<0.001	-0.42	0.677	3.41	0.003

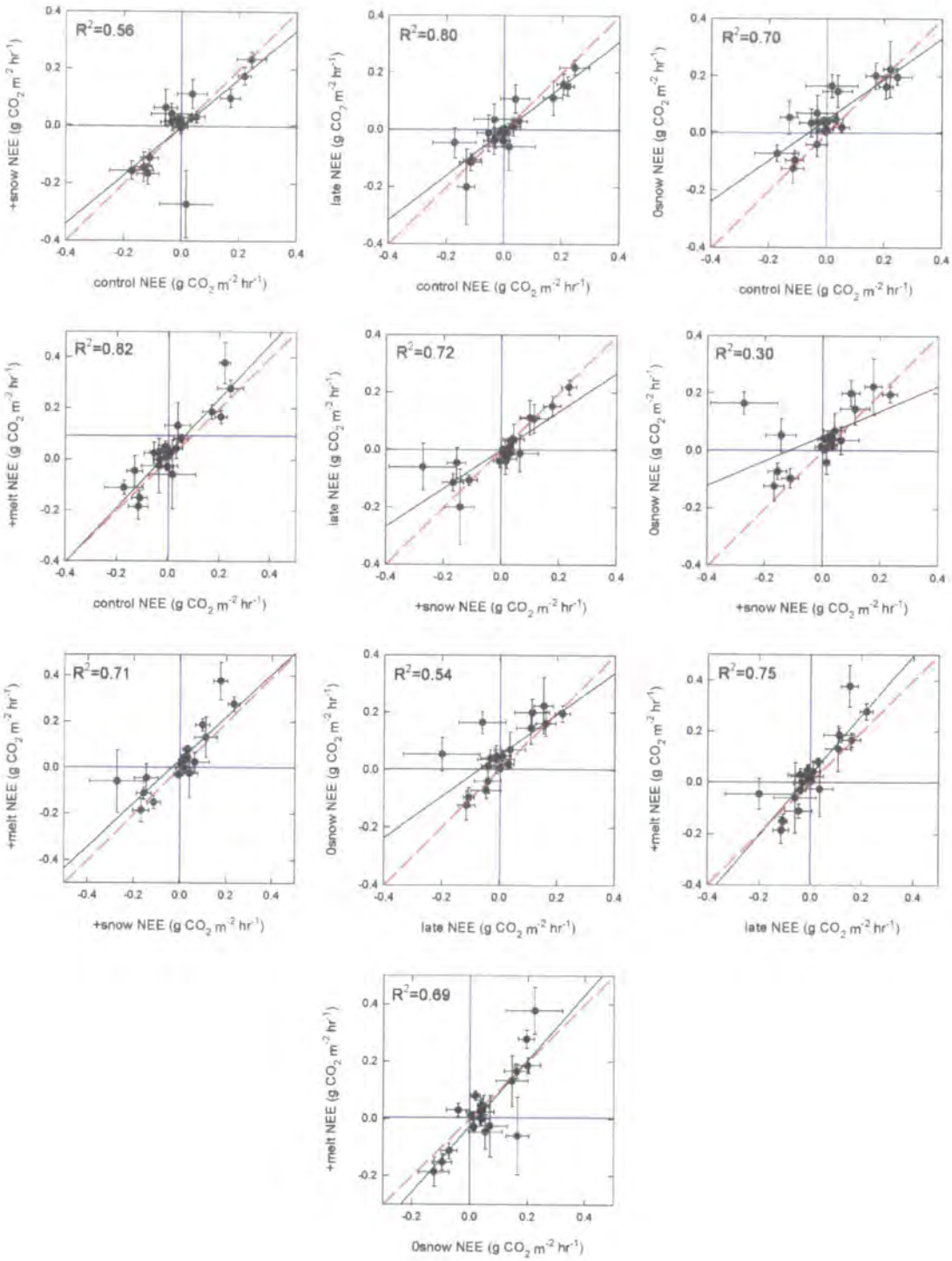

Figure 5-14: Pairwise treatment vs. treatment mean NEE (± standard error; n=5). The red dashed lines indicate the position of a 1:1 relationship while the black solid lines indicate the line of best fit. The blue solid lines indicate the compensation point.

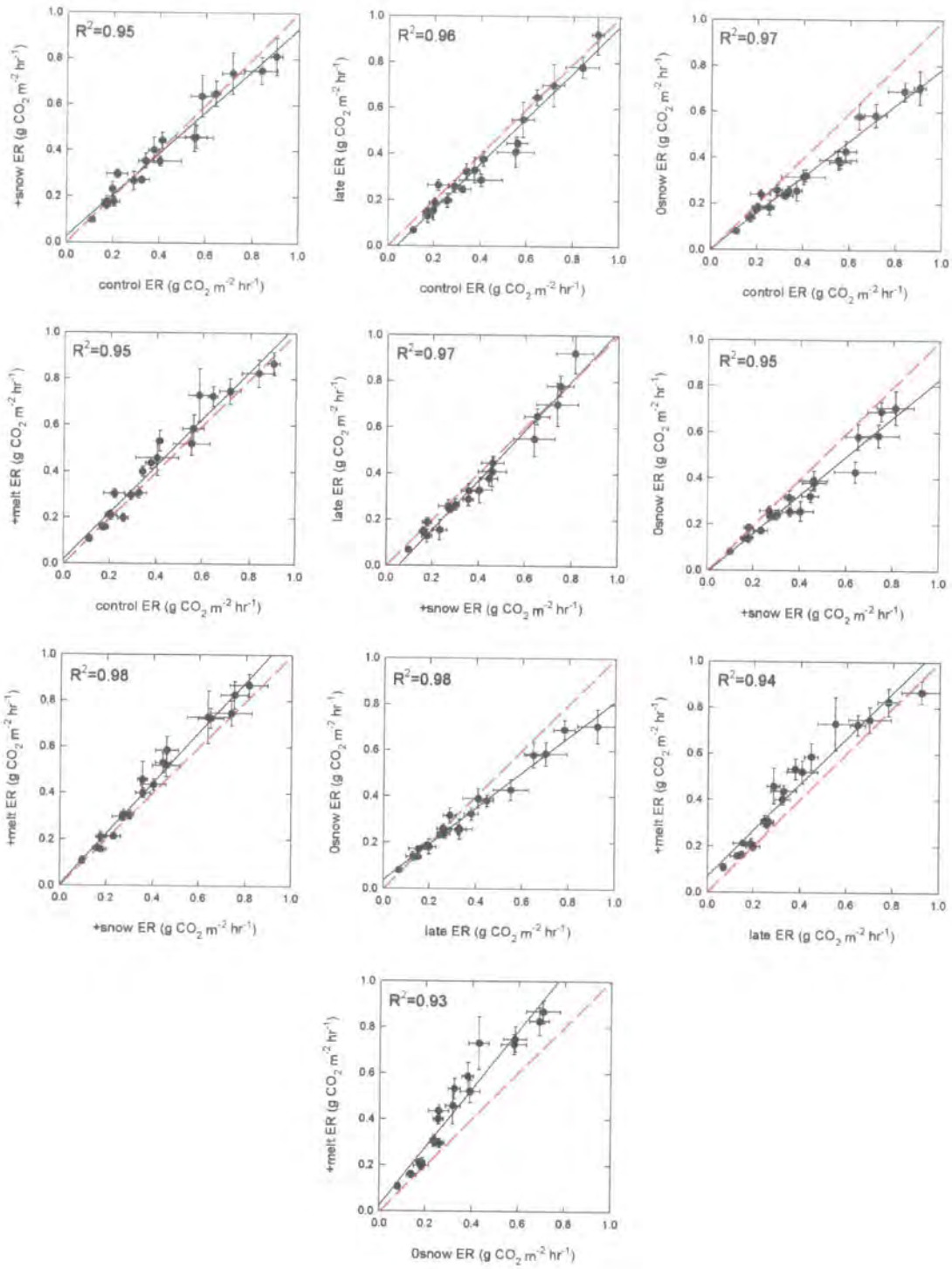

Figure 5-15: Pairwise treatment vs. treatment mean ER (± standard error; n=5). The red dashed lines indicate the position of a 1:1 relationship while the black solid lines indicate the line of best fit.

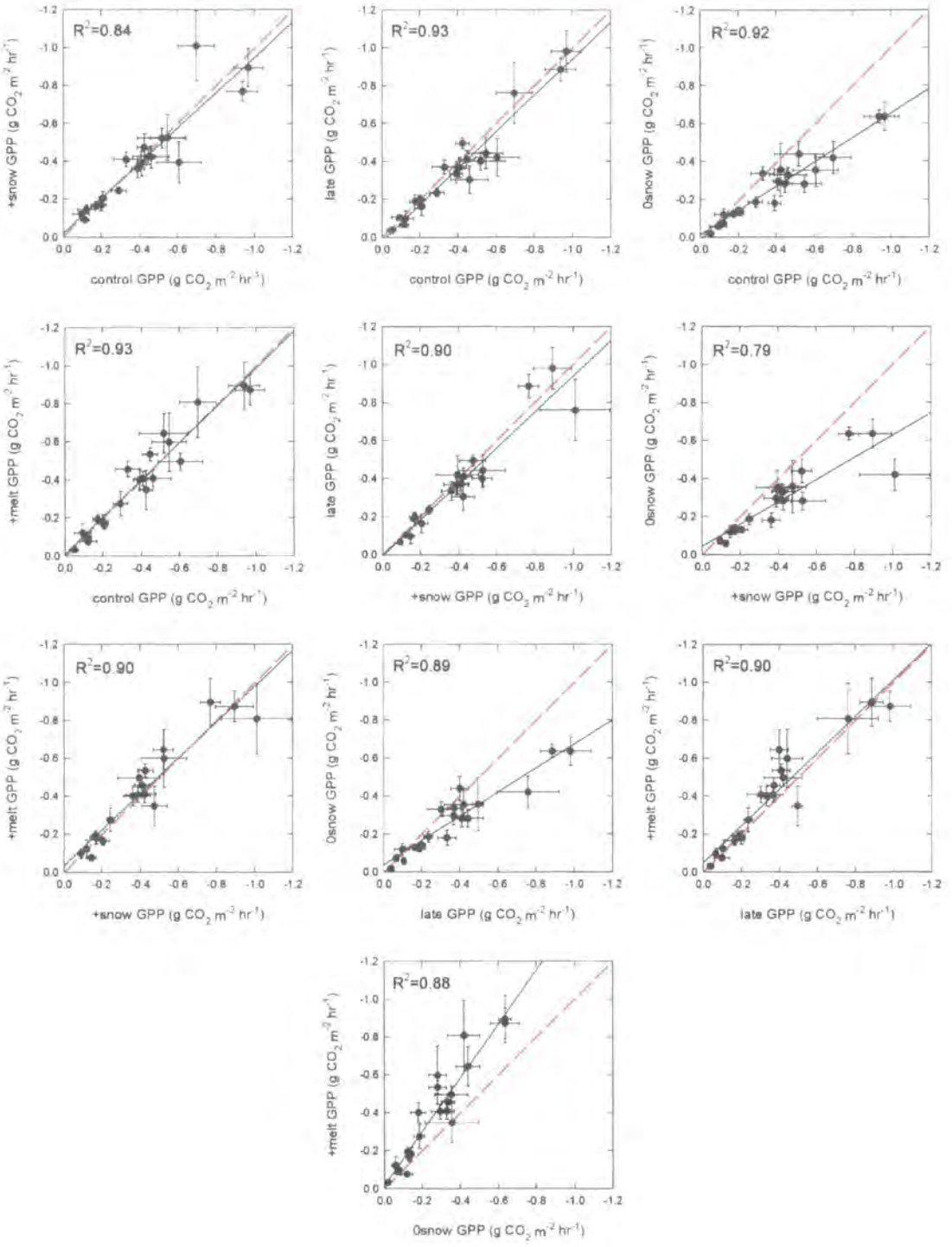

Figure 5-16: Pairwise treatment vs. treatment mean GPP (± standard error; n=5). The red dashed lines indicate the position of a 1:1 relationship while the black solid lines indicate the line of best fit.

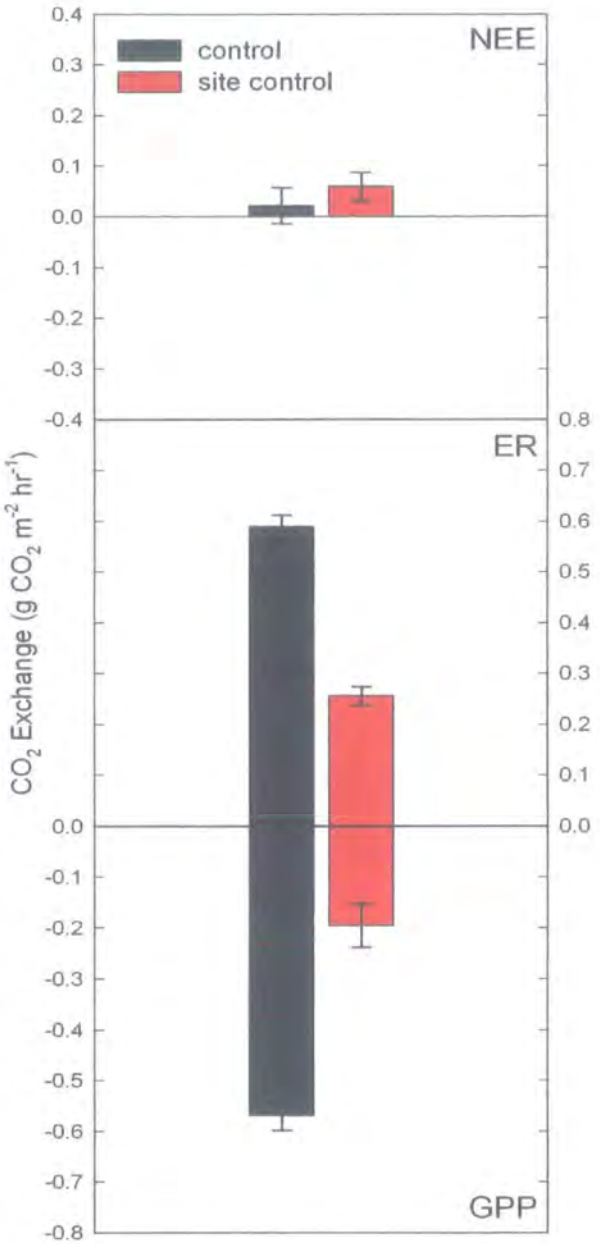

Figure 5-17: Monolith site comparison mean CO_2 exchange (± standard error; n=5).

For logistical reasons, it was only possible to conduct comparative measurements of CO_2 exchange for the 'site control' and 'control' treatments on one occasion (when a helicopter was available). On this occasion, both ER and GPP were significantly greater (more negative in the case of GPP) in the 'control' treatment than in the 'site control' (t=11.76, -7.11; P<0.001, <0.001; for ER and GPP respectively) (see Figure 5-17). There was however, no significant difference between the two treatments in the resulting NEE (t=-0.83, P=0.433).

CHAPTER 6: MODELLING OF ECOSYSTEM CARBON DIOXIDE EXCHANGE

6.1 THE MODEL

This study employs a modified version of the surface CO_2 flux model used by Lloyd (2001) for modelling the net ecosystem productivity of a High Arctic polar semi-desert site in Svalbard. This was itself composed of two established models that independently describe the respective CO_2 flux activities of the aboveground and belowground components of an ecosystem. The belowground component is described by the soil respiration model of Lloyd and Taylor (1994), while the aboveground component is described by the C_3 photosynthesis model developed by Cox et al. (1998, 1999), as part of the UK Meteorological Office Surface Exchange Scheme (MOSES), which is in turn based upon the work of Collatz (1991). Lloyd (2001) extended these existing model components to account for the behaviour of the cryptogams that occupied a large proportion of his High Arctic study site. Here, further modifications have been made to account for the influences of snow cover and plant phenology in an attempt to model the ecosystem CO_2 exchange of the three study communities at the STEPPS fieldsite for 2003 and 2004.

6.1.1 Structure

The model calculates hourly values of net ecosystem CO_2 exchange (*NEE*) as:

$$NEE = R + W$$

Equation 6-1

where W is photosynthesis (equivalent to GPP) and R is whole ecosystem respiration (equivalent to ER). R consists of both belowground respiration (R_s ; plant roots and microbes) and aboveground respiration (R_d ; plant leaves/stems):

$$R = R_s + R_d$$

Equation 6-2

In the model, the community is divided into three tiles: Bare ground, cryptogams, and vascular plants. W and R_d are calculated differently for each tile and weighted according to the respective proportions of the community that they make up:

$$W = \frac{(W_{cryp}C_{cryp}) + (W_{vasc}C_{vasc})}{100}$$

Equation 6-3

$$R_d = \frac{(R_{d_{cryp}}C_{cryp}) + (R_{d_{vasc}}C_{vasc})}{100}$$

Equation 6-4

where C_{cryp} and C_{vasc} are the percentage ground cover of cryptogams and vascular plants respectively. For the vascular plants, W and R_d, as calculated by equations 3 to 23 in the Appendix, are adjusted according to soil moisture:

$$W_{vasc} = W_{wet}\beta_s$$

Equation 6-5

$$R_{d_{vasc}} = R_{d_{wet}}\beta_s$$

Equation 6-6

where W_{wet} and $R_{d_{wet}}$ are the non moisture-limited rates of photosynthesis and leaf respiration respectively. These rates are also adjusted according to plant phenological status:

$$W_{vasc} = W_{1PPI}PPI$$

Equation 6-7

$$R_{d_{vasc}} = R_{d_{1PPI}}PPI$$

Equation 6-8

where PPI is the plant phenological index, a scaling factor which ranges from zero, when there are no leaves, to one, at peak leaf extension. W_{1PPI} and $R_{d_{1PPI}}$ are the respective rates of photosynthesis and leaf respiration when $PPI = 1$. The vascular plant tile is further subdivided into a deciduous tile with a variable PPI and an evergreen tile where PPI remains constant. Thus, equations 6-7 and 6-8 become:

$$W_{vasc} = (W_{1PPI} PPI_D C_D) + (W_{1PPI} C_{Ev})$$

Equation 6-9

$$R_{d_{vasc}} = (R_{d_{1PPI}} PPI_D C_D) + (R_{d_{1PPI}} C_{Ev})$$

Equation 6-10

The determination of foliar phenology has been shown to be an important factor in the modelling of Arctic tundra carbon balance (van Wijk et al. 2003b), but leaf phenology has thus far proven difficult to parameterise due to incomplete understanding of the processes involved (Arora & Boer 2005). Here, the phenological cycle "begins" with a temperature-dependent growth phase similar to that of the LPJ DGVM (Lund-Potsdam-Jena Dynamic Global Vegetation Model) (Sitch et al. 2003). During the growth phase, PPI_D is given as:

$$PPI_D = PPI_{D_{-1}} + g_{T_c}$$

Equation 6-11

where g_{T_c} is the asymptotic, temperature-dependent hourly growth increment, given as either:

$$g_{T_c} = \left(\frac{T_c}{5} g\right) 1 - PPI_{D_{-1}}$$

Equation 6-12

where g is a constant growth (leaf area expansion) factor, or as zero when either the soil is frozen or leaf temperature is below zero. For the growth phase to begin, a chill sum of 336 hours (two weeks) of leaf temperatures below -5°C must be exceeded. This figure was chosen arbitrarily, and is included solely to prevent re-initiation of growth after completion of senescence during periods of warmth in the autumn. It has been assumed that any actual chilling requirements for the cessation of winter dormancy would easily be met under current climatic conditions (Pop et al. 2000). The growth phase is followed by a senescence phase, during which PPI_D is given as:

$$PPI_D = PPI_{D_{-1}} - s$$

Equation 6-13

where s is a constant senescence factor. The actual processes that determine the onset of foliar senescence are less well understood than those governing growth initiation (van Wijk et al. 2003b), but evidence suggests that strategies based on day/night length are the most efficient for northern woody plants (Hänninen et al. 1990). Therefore, assuming optimal adaptation of the plants at the fieldsite, the model senescence phase is triggered either by decline in day length beyond a defined community dependent limit (using day number, S, as a proxy for day length), or by a severe frost (leaf temperature below -10 °C) if that occurs first.

For the cryptogams, the values of W and R_d are adjusted according to the lower photosynthetic capacity of cryptogams compared to vascular plants:

$$W_{cryp} = 0.1W$$

Equation 6-14

and leaf/thallus water status:

$$W_{cryp} = W_{cryp_{wet}} \beta_{cryp}$$

Equation 6-15

where $W_{cryp_{wet}}$ is the non moisture-limited rate of cryptogam photosynthesis and β_{cryp} is the cryptogam moisture factor (between zero and one).

6.1.2 Parameters and Calibration

The values for the state parameters common to all three of the communities being modelled are the same as those used by Lloyd (2001) (see Appendix) and hence, in the case of the photosynthesis parameters, do not differ from the default values within the standard MOSES model. Values for the community dependent state parameters (see Table 6-1) were selected on the basis of their optimising influence on model performance (see section 6.2), when compared with observed CO_2 flux values from a selected location within each community for the 2003 snow-free season.

Table 6-1: Community specific state parameters

Name	Description	Unit	Value
Fen			
C_{cryp}	Cryptogam cover	%	42
C_{vasc}	Vascular plant cover	%	42
C_D	Deciduous plant cover	%	100
C_{Ev}	Evergreen plant cover	%	0
g	Growth factor	-	0.006
R_{10}	Rate of soil respiration at 10°C	µmol CO_2 m^{-2} s^{-1}	2.2
S	Senescence start date	Day of year	225
s	Senescence factor	-	0.00075
θ_{crit}	Critical soil moisture	m^3 H_2O m^{-3}	0.12
Heath			
C_{cryp}	Cryptogam cover	%	25 (40)
C_{vasc}	Vascular plant cover	%	27 (60)
C_D	Deciduous plant cover	%	60 (65)
C_{Ev}	Evergreen plant cover	%	40 (35)
g	Growth factor	-	0.001
R_{10}	Rate of soil respiration at 10°C	µmol CO_2 m^{-2} s^{-1}	1.8 (2.3)
S	Senescence start date	Day of year	240
s	Senescence factor	-	0.00075
θ_{crit}	Critical soil moisture	m^3 H_2O m^{-3}	0.08
Ridge			
C_{cryp}	Cryptogam cover	%	15
C_{vasc}	Vascular plant cover	%	15
C_D	Deciduous plant cover	%	80
C_{Ev}	Evergreen plant cover	%	20
g	Growth factor	-	0.001
R_{10}	Rate of soil respiration at 10°C	µmol CO_2 m^{-2} s^{-1}	0.7
S	Senescence start date	Day of year	250
s	Senescence factor	-	0.00075
θ_{crit}	Critical soil volumetric water content	m^3 H_2O m^{-3}	0.11

Table 6-2: Driving parameters

Name	Description	Unit	Source
Common			
P	Atmospheric pressure	Pa	MOP4
RH	Relative humidity	%	MOP4
R_n	Net radiation flux	W m^{-2}	MOP4
SW	Incident shortwave radiation	W m^{-2}	MOP4
T_A	Air temperature	K	MOP4
$Rain$	Rainfall	mm	MOP4
Fen			
SI	Snow cover index	-	Surveys
T_s	Near surface soil temperature	K	MOP1
θ	Near surface soil volumetric water content	m^3 H_2O m^{-3}	MOP1
Heath			
SI	Snow cover index	-	Surveys
T_s	Near surface soil temperature	K	MOP4
θ	Near surface soil volumetric water content	m^3 H_2O m^{-3}	MOP5
Ridge			
SI	Snow cover index	-	Surveys
T_s	Near surface soil temperature	K	MOP4
θ	Near surface soil volumetric water content	m^3 H_2O m^{-3}	MOP7

Hourly values for each of the model driving parameters (see Table 6-2 and Figure 6-1), with the exception of snow cover index (SI), were obtained from the most appropriate MOP at the STEPPS fieldsite respectively. During periods of logger and/or sensor failure, data gaps were filled with either averages of adjacent values or data from the next most appropriate MOP, depending both on the length of the gap, and the availability of suitable substitute data sources. P, RH and T_A were all measured at MOP4 using a HMP45AC probe (Vaisala Ltd, Suffolk, UK) mounted at approximately 2 m. R_n and SW were also measured at MOP4 at approximately 2 m, using an NR LITE net pyrgeometer and CM5 pyranometer respectively (Kipp & Zonen Ltd, Lincolnshire, UK). T_s was measured at MOP4 and MOP1 at depths of approximately 5 cm using custom made thermocouple ring frost gauges (CEH Wallingford, UK). θ was measured at MOP1, MOP5 and MOP7 at

depths of approximately 15 cm using CS616-L Water Content Reflectometers (Campbell Scientific Ltd, Leicestershire, UK). All hourly averages were derived from half hourly averages logged by CR10X dataloggers (Campbell Scientific Ltd, Leicestershire, UK) at each respective MOP. Values for *SI* were obtained by manual observation during the snow surveys described in section 3.1.3. For periods when the relevant plots had snow cover index values below four (i.e. >10% snow cover), T_A and *SW* were both adjusted accordingly to account for the insulative and reflective properties of the snow layer, so that T_A was equal to T_s and *SW* became zero.

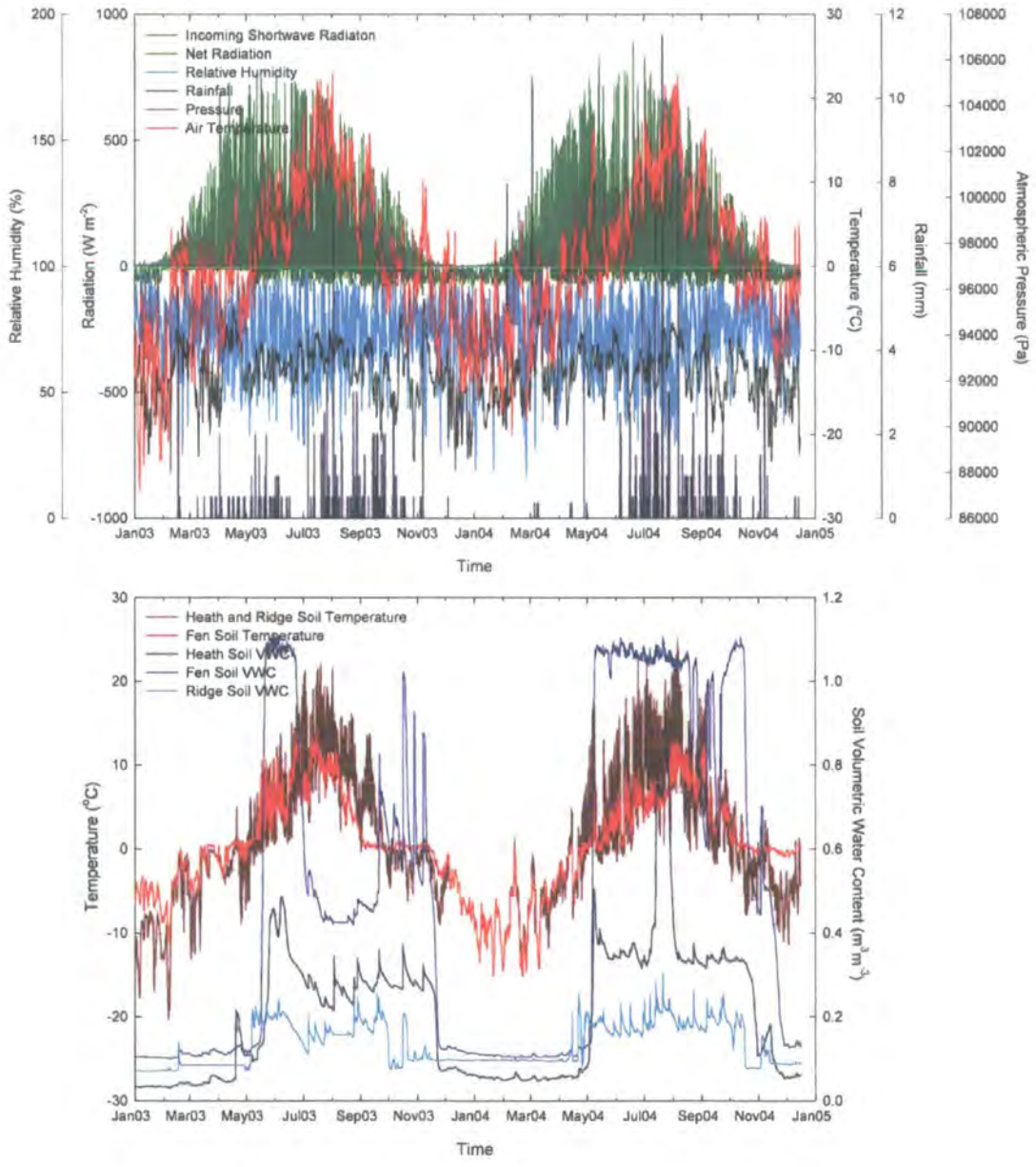

Figure 6-1: Hourly values of the variable (driving) model parameters.

6.2 MODEL PERFORMANCE

6.2.1 Observation Data

In order to assess the performance of the model, the estimated values of ecosystem CO_2 exchange were compared with selected observed values from the flux surveys conducted throughout the snow-free seasons of 2003 and 2004 (see section 3.1.6). For each of the three communities being studied, one 'control' plot was selected as a representative with which the model could be calibrated and tested. In each case, the comparison plot was selected for each community by comparing the values of NEE, ER and GPP from each of the plots with their community means. The three plots which were most similar to their respective community means were selected; these were 'Fen control 3', 'Heath control 1' and 'Ridge control 1' (see Figure 6-2). The observed CO_2 exchange data from these plots are displayed in Figure 6-3. It must be noted that, as a result of the vegetation damage caused by the insertion of the flux collars in the Heath community in 2003, the 2004 data for this community were taken from the replacement collar at the same plot.

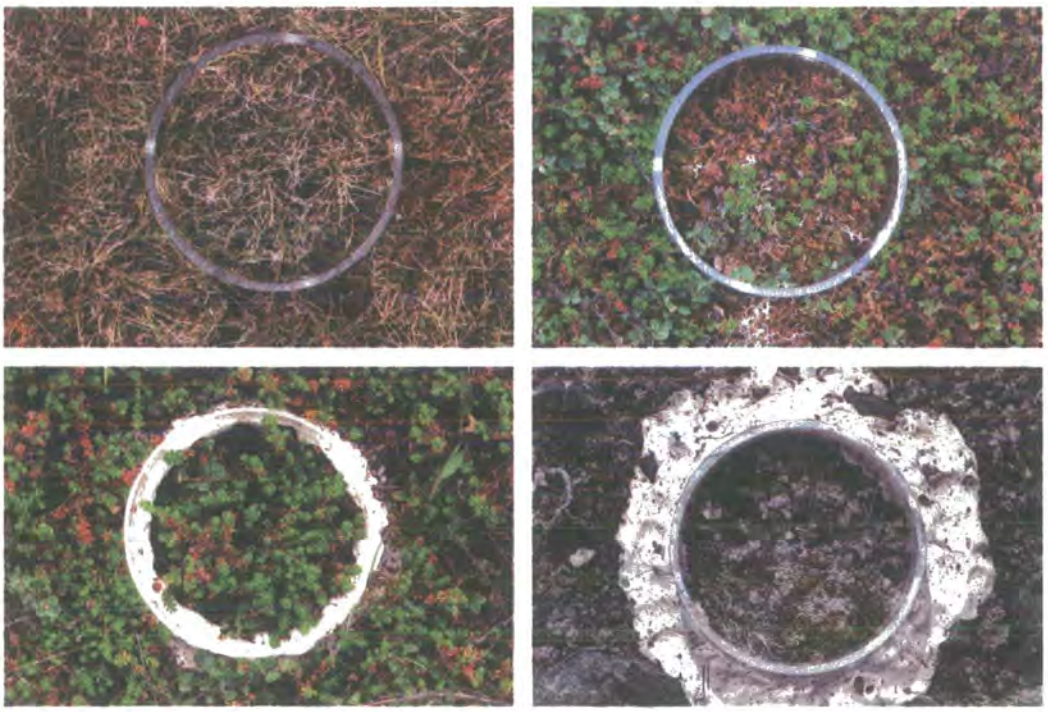

Figure 6-2: The representative plot flux collars on 27/07/04; Fen control 3 (top left), 2003 Heath control 1 (top right), 2004 Heath control 1 (bottom left) and Ridge control 1 (bottom right).

In addition to the observation data obtained as part of the field experiment, CO_2 exchange measurements were also taken during three diel cycles at contrasting points throughout the 2004 growing season (2-3 June, 16-17 July and 25-26 August); enabling a more detailed evaluation of the model's performance at a finer temporal scale, during the night as well as the day. The methodology employed for these diel surveys followed that described in section 3.1.6, with the exception that measurements were taken once every three hours from noon until noon again, and only at the representative plots for each community. The data from these three surveys are displayed in Figure 6-4.

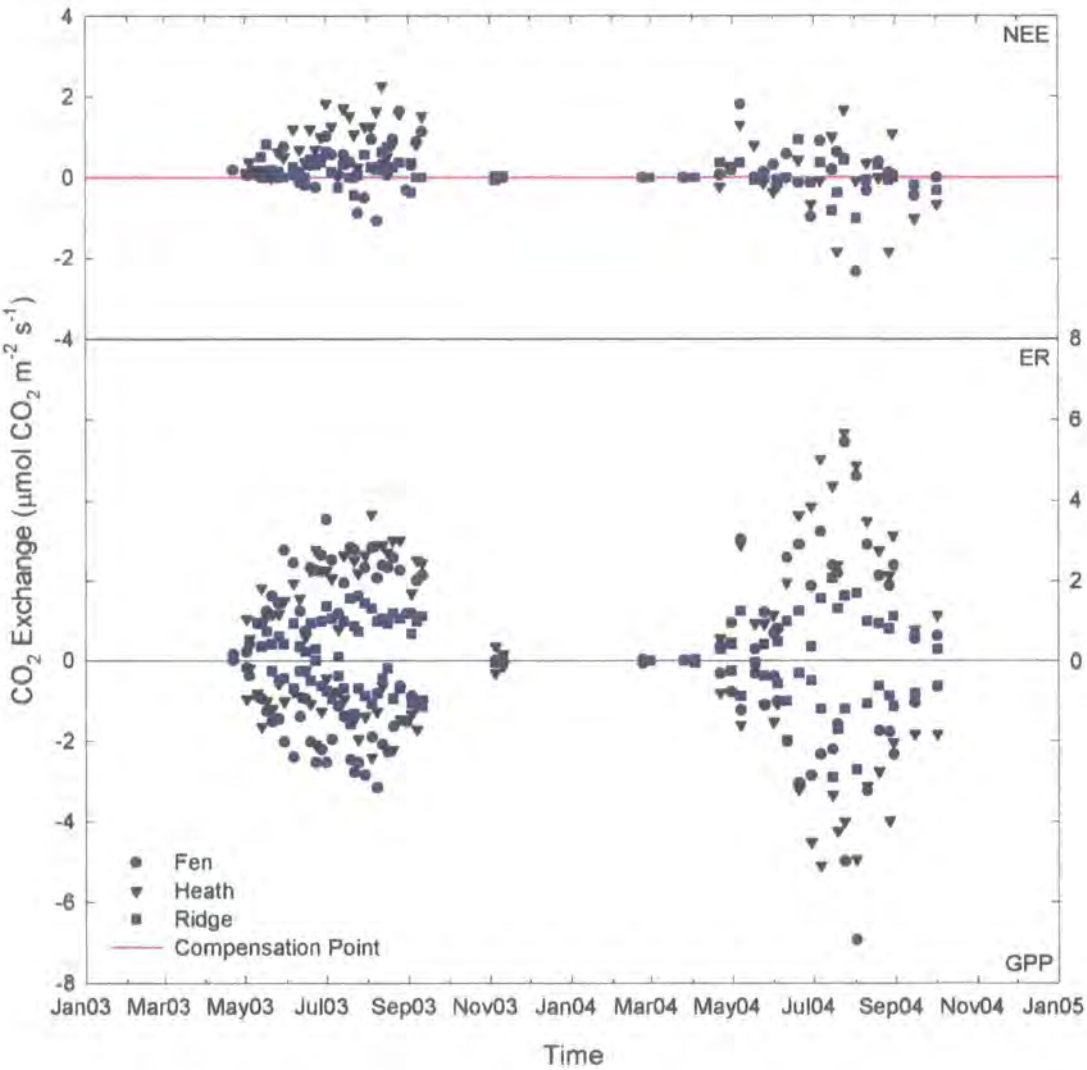

Figure 6-3: Observed CO_2 exchange values for the representative plots of the three communities being modelled.

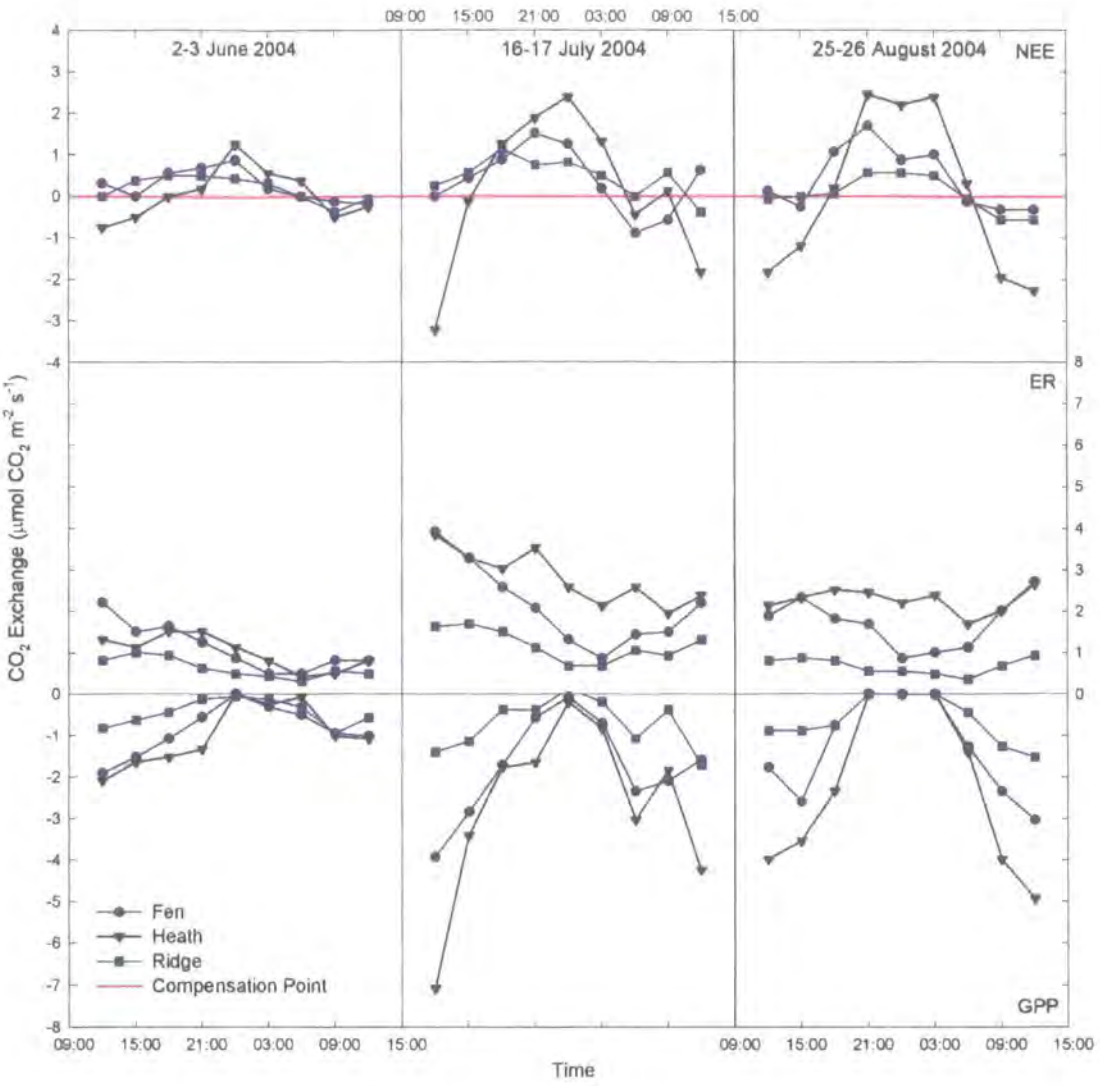

Figure 6-4: Diel CO_2 exchange values for the representative plots of the three communities being modelled.

6.2.2 Statistical Evaluation

A quantified comparison of the model outputs with the observed data was achieved using the method recommended by Willmott (1984), whereby the Degree of Agreement Index (*d*) is calculated as:

$$d = 1 - \frac{N \cdot RMSE^2}{\sum_{i=1}^{N} \left(\left(M_i - \overline{O} \right) + \left(O_i - \overline{O} \right) \right)^2}$$

Equation 6-16

where N is the number of observations, M and O are the modelled and observed values respectively and *RMSE* is the root mean square error (in μmol CO_2 m^{-2} s^{-1} in this instance), given as:

$$RMSE = \sqrt{\left(N^{-1} \sum_{i=1}^{N} (M_i - O_i)^2 \right)}$$

Equation 6-17

Values for d can range from zero, where there is no agreement between the modelled and observed values, and one, where the model output and observations are in complete agreement. A good model will therefore give high d values with low *RMSE*. This evaluation technique is analogous to Pearson's product-moment correlation, but superior for this purpose due to the fact that it takes into account proportional and additive differences between M and O, as well as the degree of co-linearity between the two sets of values.

The model's performance was evaluated for each of the three CO_2 flux variables (R, W and *NEE*) in turn in each of the three study communities. First the performance of the model was optimised against the 2003 observed data by tuning of the community-specific parameters given in Table 6-1. The calibrated model was then tested against the 2004 observations (seasonal and diel) to assess its predictive capabilities.

6.2.3 Ecosystem Respiration

Performance of the calibrated model for R in 2003 was found to be similar for each community, with fairly high d values given for all three (see Table 6-3, Figure 6-5 and Figure 6-6). *RMSE* was also fairly high however; with values equivalent to ~30% of $\overline{O}$ in each case.

Table 6-3: Model performance for respiration (season data).

Community	2003		2004	
	d	RMSE	*d*	RMSE
Fen	0.90	0.52	0.91	0.64
Heath	0.87	0.59	0.95	0.67
Ridge	0.88	0.26	0.91	0.31

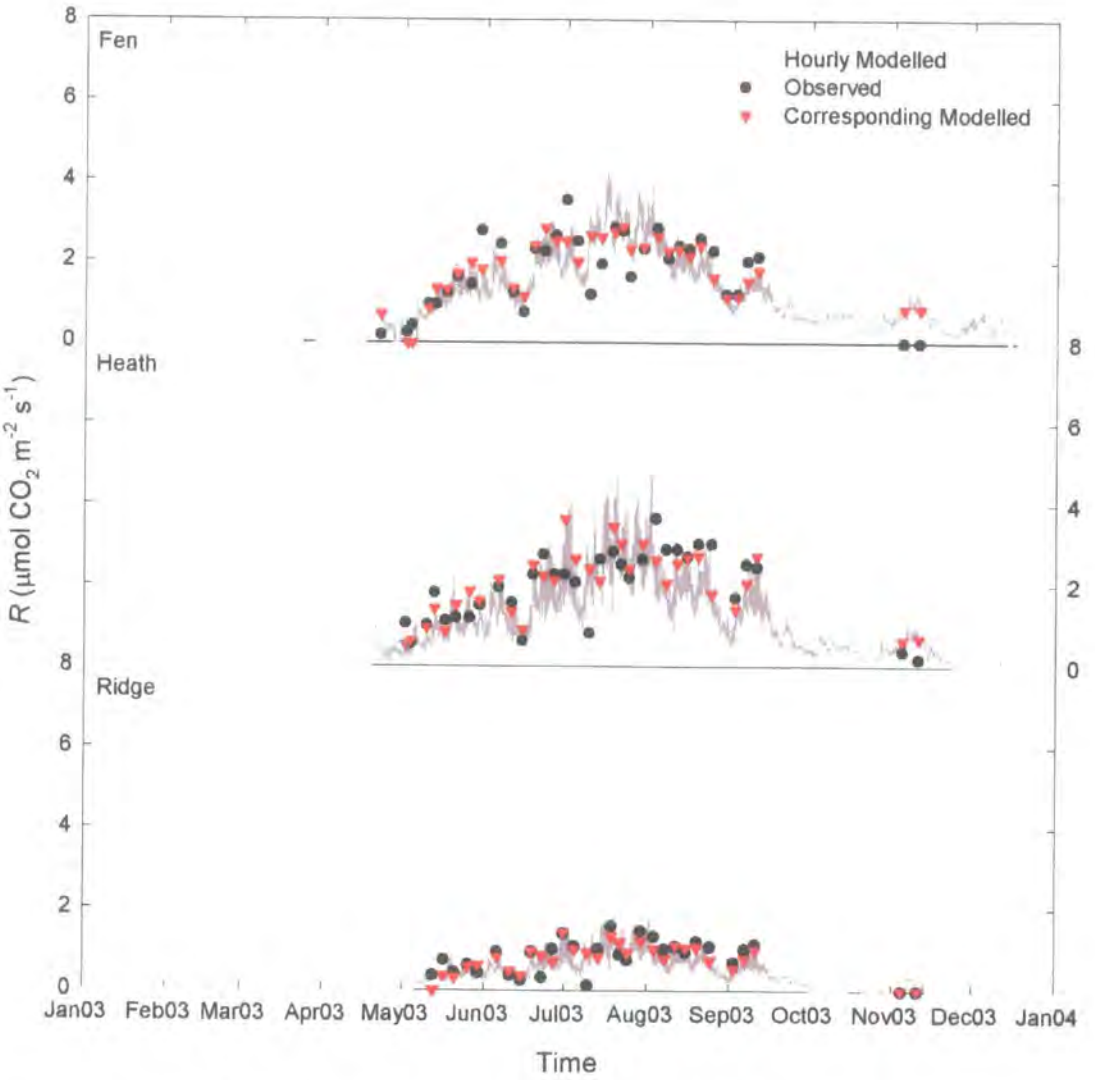

Figure 6-5: Modelled and observed values for ecosystem respiration in each of the three study communities, 2003.

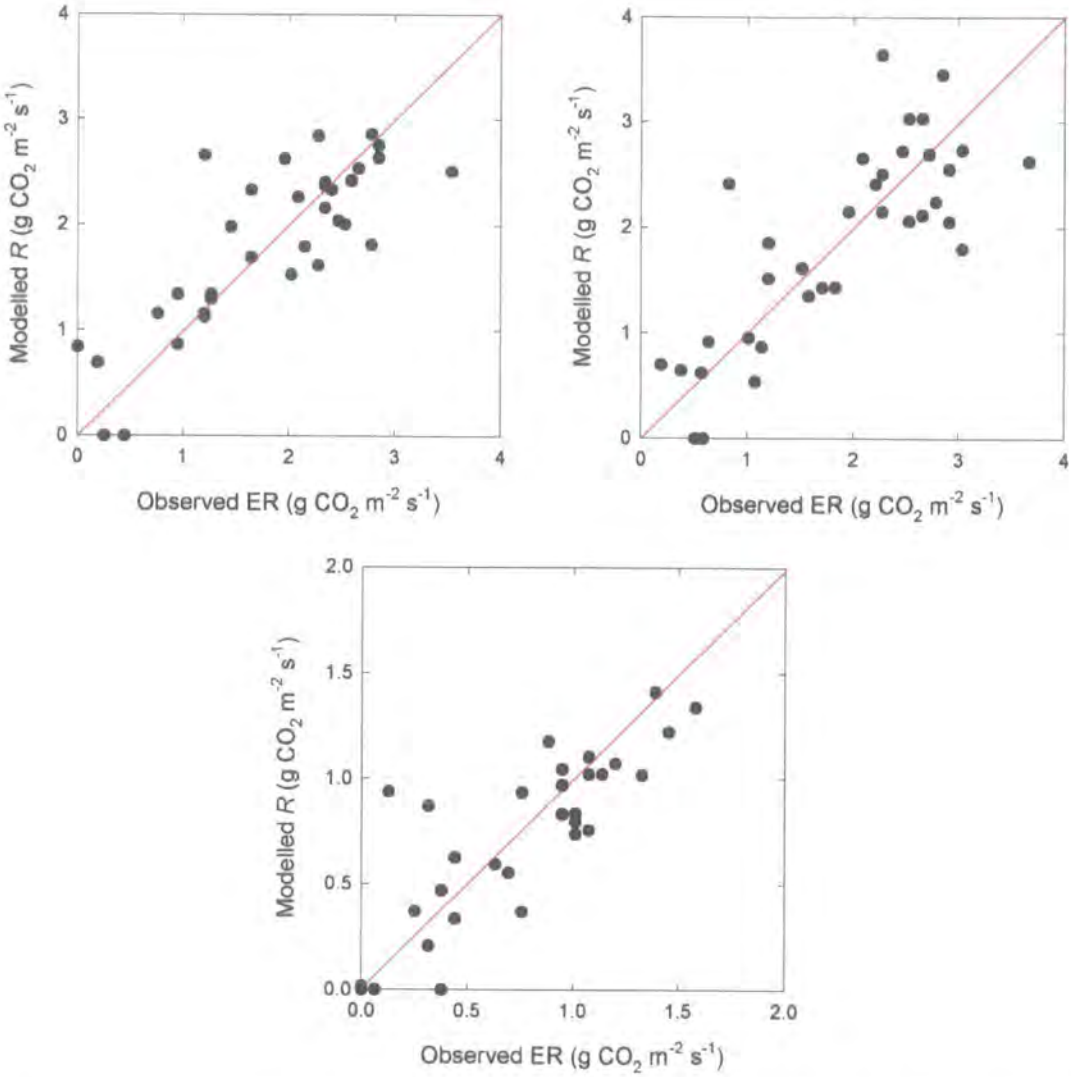

Figure 6-6: Observed vs. modelled ecosystem respiration for the Fen (top left), Heath (top right) and Ridge (bottom) communities, 2003. The red line indicates the position of a 1:1 relationship.

When tested against the 2004 season respiration data, performance of the model was found to improve in all three communities, with higher *d* values than for 2003 in each case (see Table 6-3, Figure 6-7 and Figure 6-8). In some cases, *RMSE* was also higher however, ranging from 26 to 41% of $\overline{O}$.

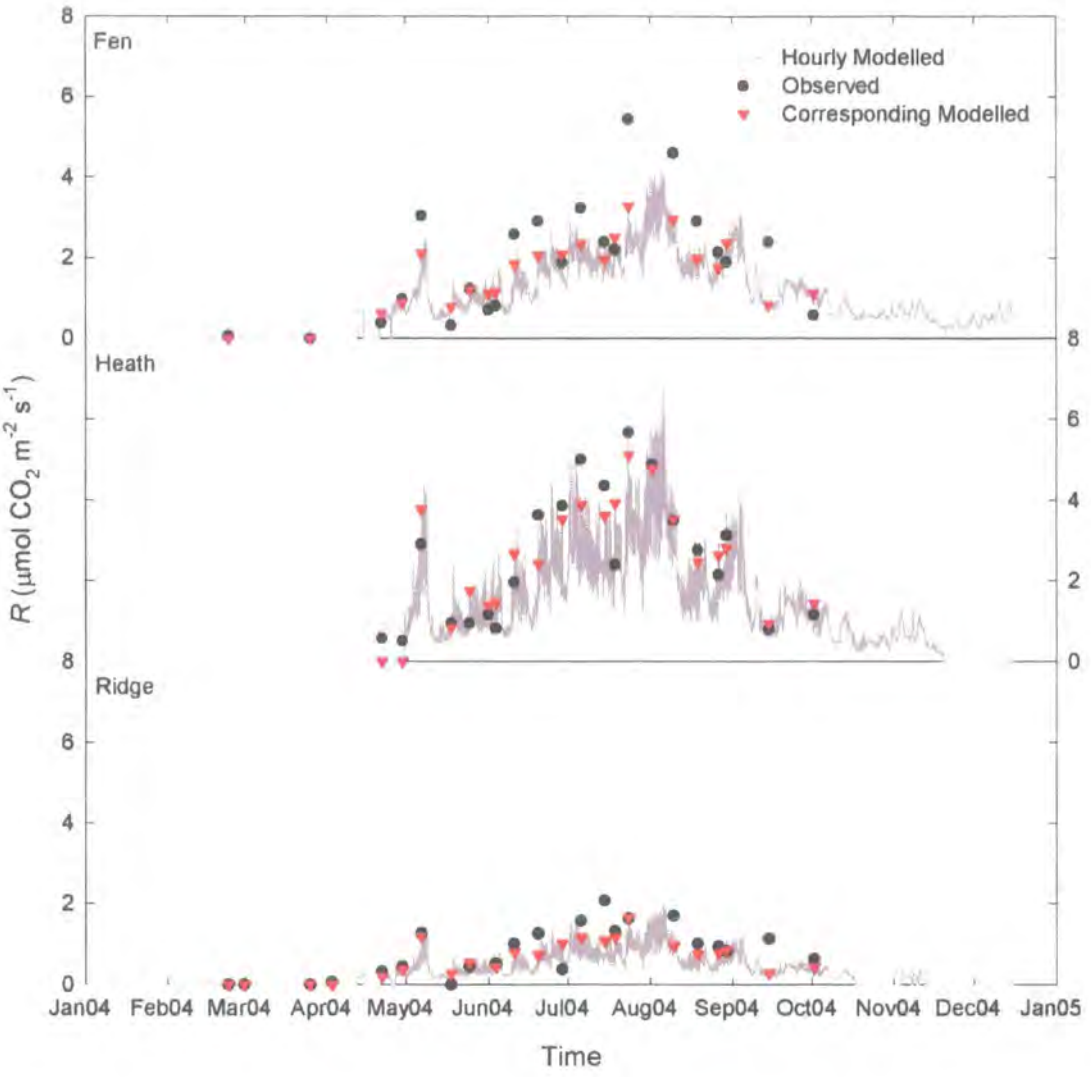

Figure 6-7: Modelled and observed values for ecosystem respiration in each of the three study communities, 2004.

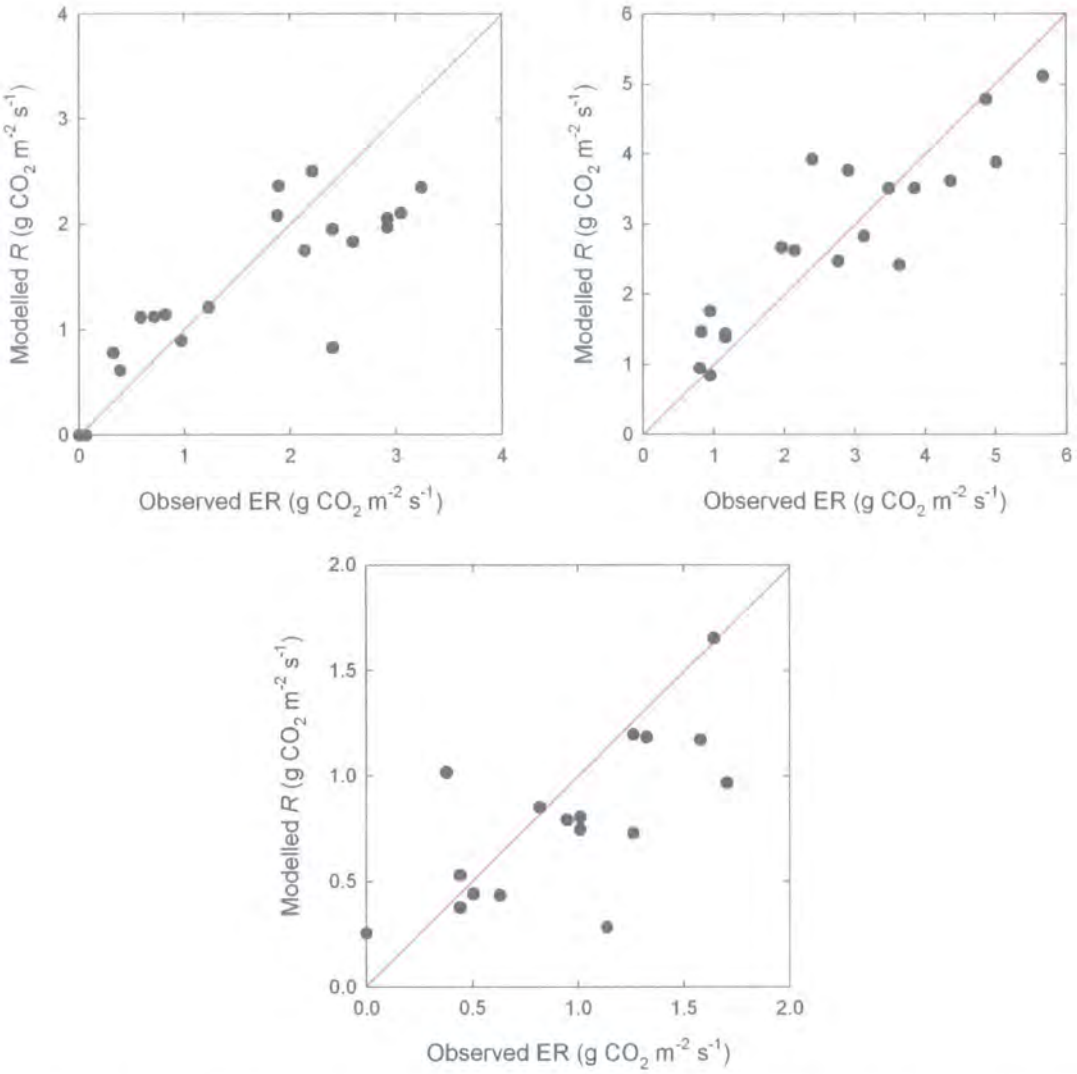

Figure 6-8: Observed vs. modelled ecosystem respiration for the Fen (top left), Heath (top right) and Ridge (bottom) communities, 2004. The red line indicates the position of a 1:1 relationship.

Performance of the model over the periods of the three diel flux surveys (Table 6-4 and Figure 6-9) was generally poorer than that observed for the season comparison, with particularly poor results for the Heath community during the June survey period, for which an *RMSE* value equivalent to 79% of $\overline{O}$ was observed. The predictions for the Heath community did improve for the July and August survey periods however, with *RMSE* values equivalent to 40% and 25% of $\overline{O}$ respectively. Although the model performed better with the Fen community than the Heath for the initial survey period, performance was poorer in July and August, with *RMSE* values equivalent to 46% and 32% of $\overline{O}$ respectively. The model's best performance over the diel study periods was with the Ridge community, where

RMSE values ranged from 22 to 49% of $\overline{O}$, with greatest error observed for the July survey period.

Table 6-4: Model performance for respiration (diel data).

Community	2-3 June		16-17 July		25-26 August	
	d	RMSE	*d*	RMSE	*d*	RMSE
Fen	0.74	0.41	0.45	0.99	0.38	0.55
Heath	0.52	0.81	0.34	1.13	0.44	0.57
Ridge	0.86	0.16	0.55	0.58	0.81	0.15

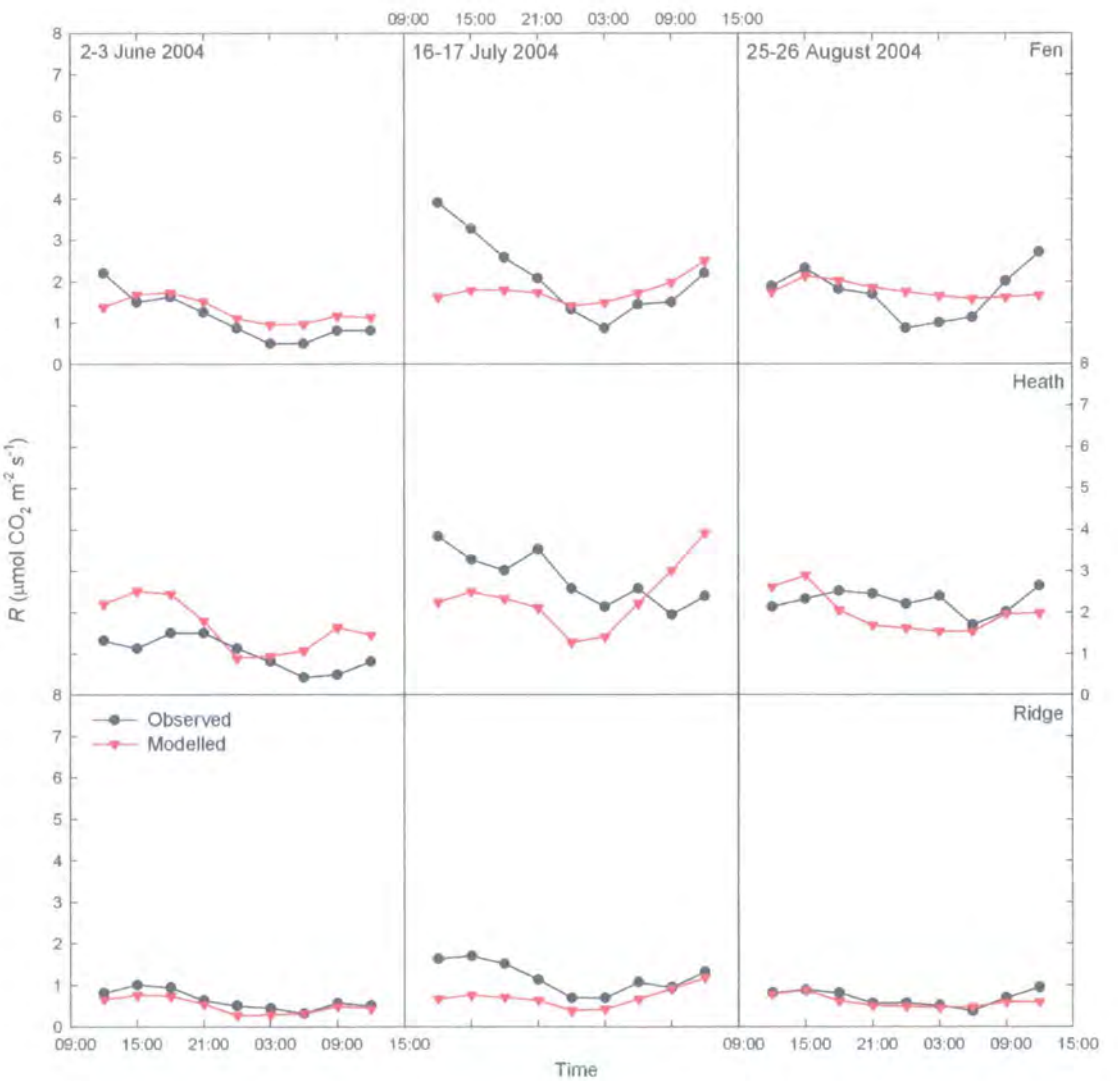

Figure 6-9: Modelled and observed values for ecosystem respiration in each of the three study communities for each of the three diel surveys.

6.2.4 *Photosynthesis*

Unlike respiration, performance of the calibrated model for W in 2003 was found to differ considerably between communities, with higher d values for the Fen than the Ridge, which in turn, had a greater d value than the Heath (see Table 6-5, Figure 6-10 and Figure 6-11). In each case, d values tended to be slightly lower than those observed for R. *RMSE* was fairly high for all three communities, although it was much lower for the Fen (28% of $\overline{O}$) than the for the Heath or Ridge (~47% of $\overline{O}$).

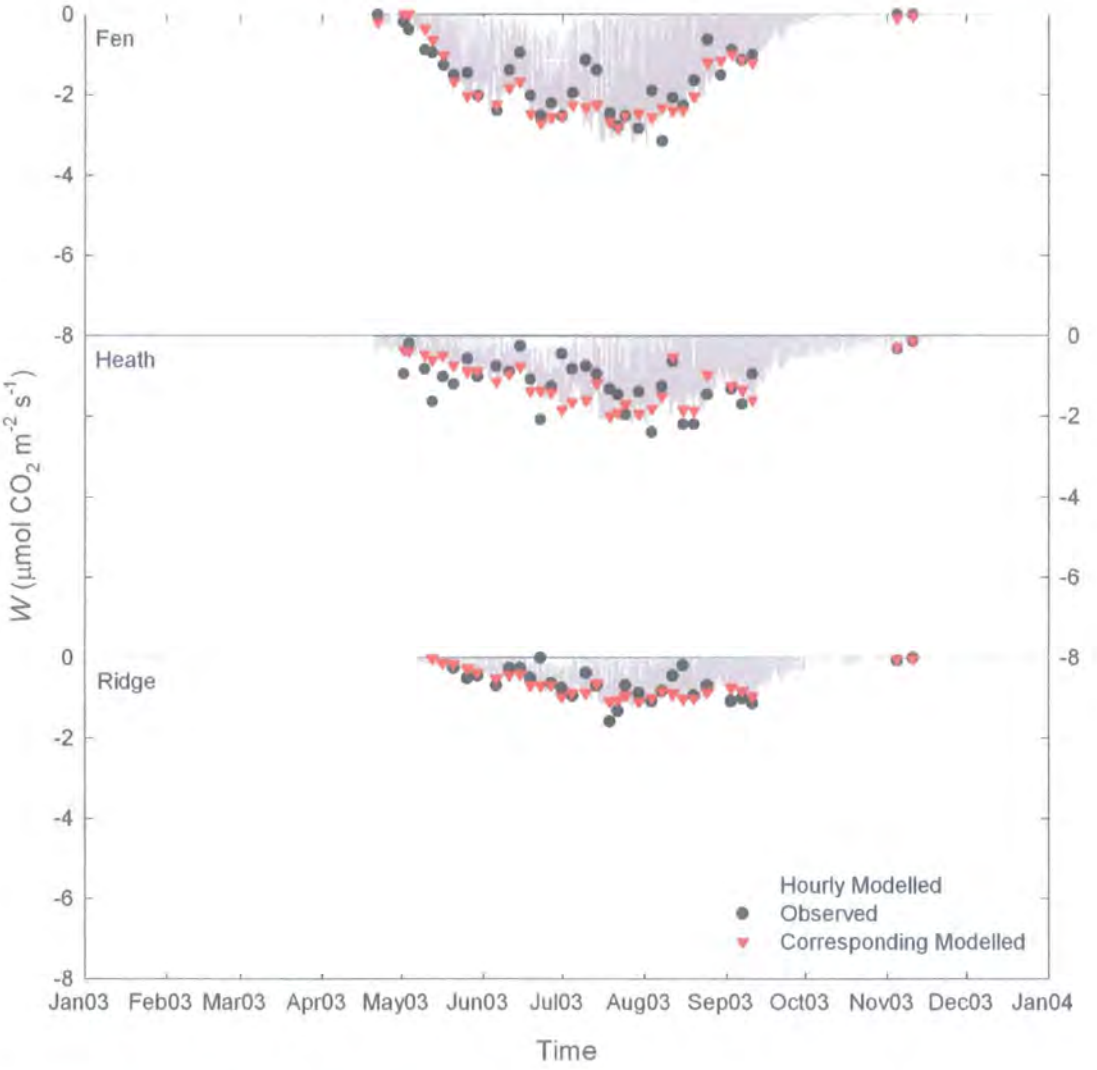

Figure 6-10: Modelled and observed values for photosynthesis in each of the three study communities, 2003.

Table 6-5: Model performance for photosynthesis (season data).

Community	2003		2004	
	d	RMSE	*d*	RMSE
Fen	0.94	0.43	0.88	0.71
Heath	0.77	0.53	0.95	0.62
Ridge	0.85	0.29	0.76	0.50

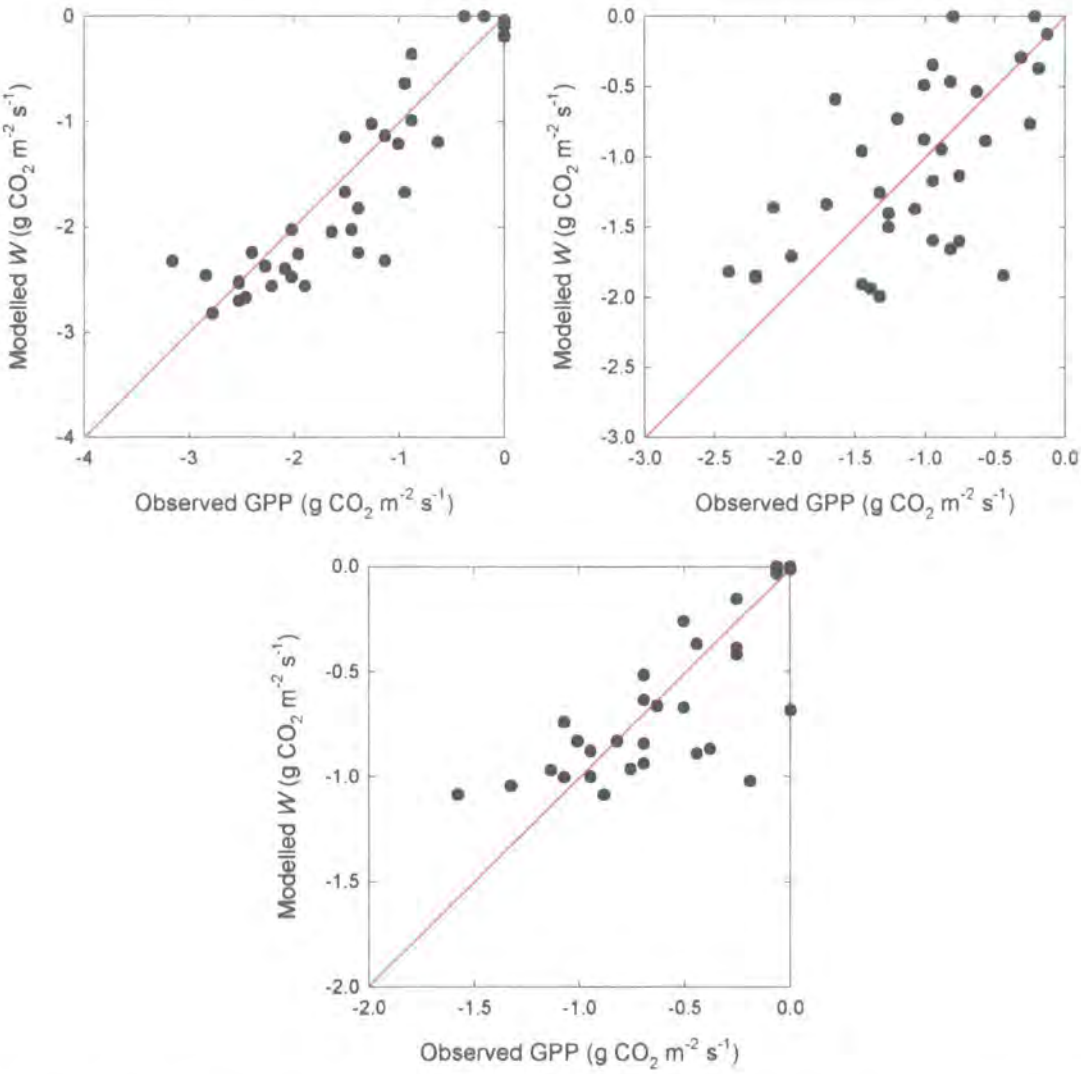

Figure 6-11: Observed vs. modelled photosynthesis for the Fen (top left), Heath (top right) and Ridge (bottom) communities, 2003. The red line indicates the position of a 1:1 relationship.

When tested against the 2004 season photosynthesis data, performance of the model, as indicated by *d*, was found to improve for the Heath community (probably due to the absence of plant damage), but became worse for the Fen and the Ridge (see Table 6-5, Figure 6-12 and Figure 6-13). *RMSE* was fairly high for all three communities, with values equivalent to 43%, 31% and 47% of $\overline{O}$ for the Fen, Heath and Ridge respectively.

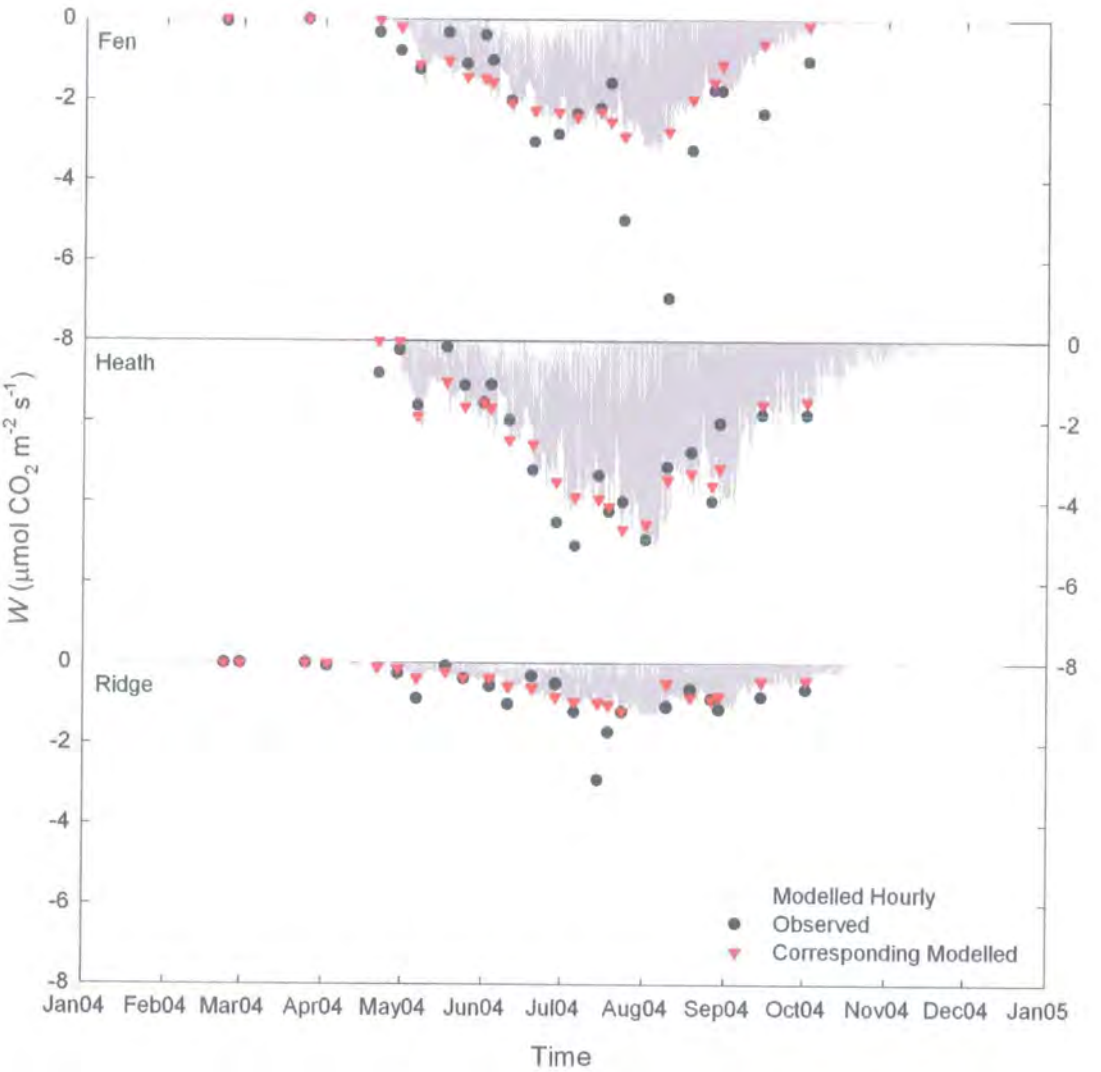

Figure 6-12: Modelled and observed values for photosynthesis in each of the three study communities, 2004.

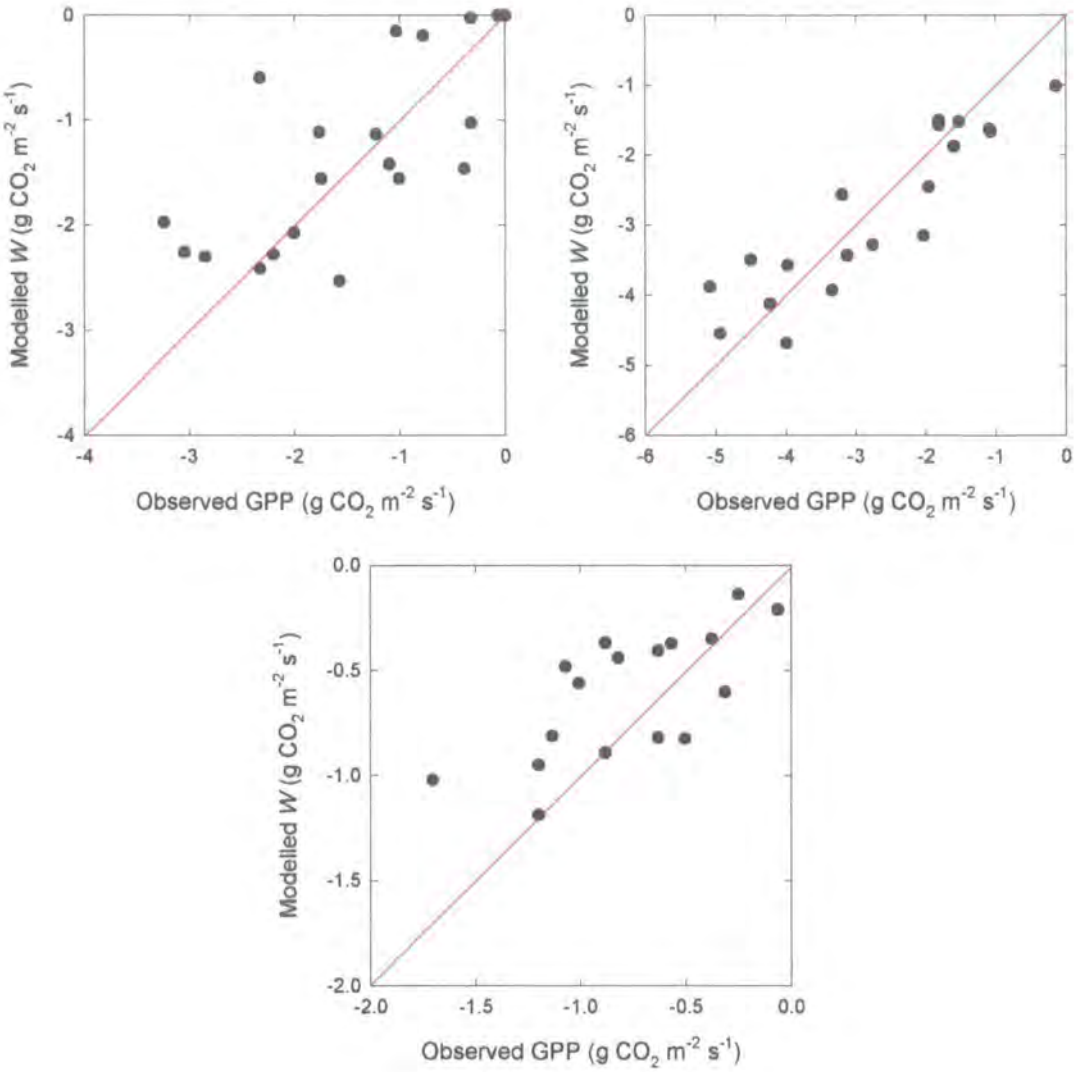

Figure 6-13: Observed vs. modelled photosynthesis for the Fen (top left), Heath (top right) and Ridge (bottom) communities, 2004. The red line indicates the position of a 1:1 relationship.

Performance of the model over the periods of the three diel flux surveys (see Table 6-6 and Figure 6-14) was generally slightly poorer than that observed for the season comparison, with better results in August than in June or July. Values of *RMSE* were fairly high throughout, ranging in the worst instance from 75% of $\overline{O}$, for the Fen community in June, to 35% of $\overline{O}$, for the Heath in August.

Table 6-6: Model performance for photosynthesis (diel data).

Community	2-3 June		16-17 July		25-26 August	
	d	RMSE	*d*	RMSE	*d*	RMSE
Fen	0.72	0.65	0.80	0.81	0.86	0.68
Heath	0.77	0.70	0.73	1.54	0.94	0.78
Ridge	0.70	0.24	0.77	0.41	0.87	0.33

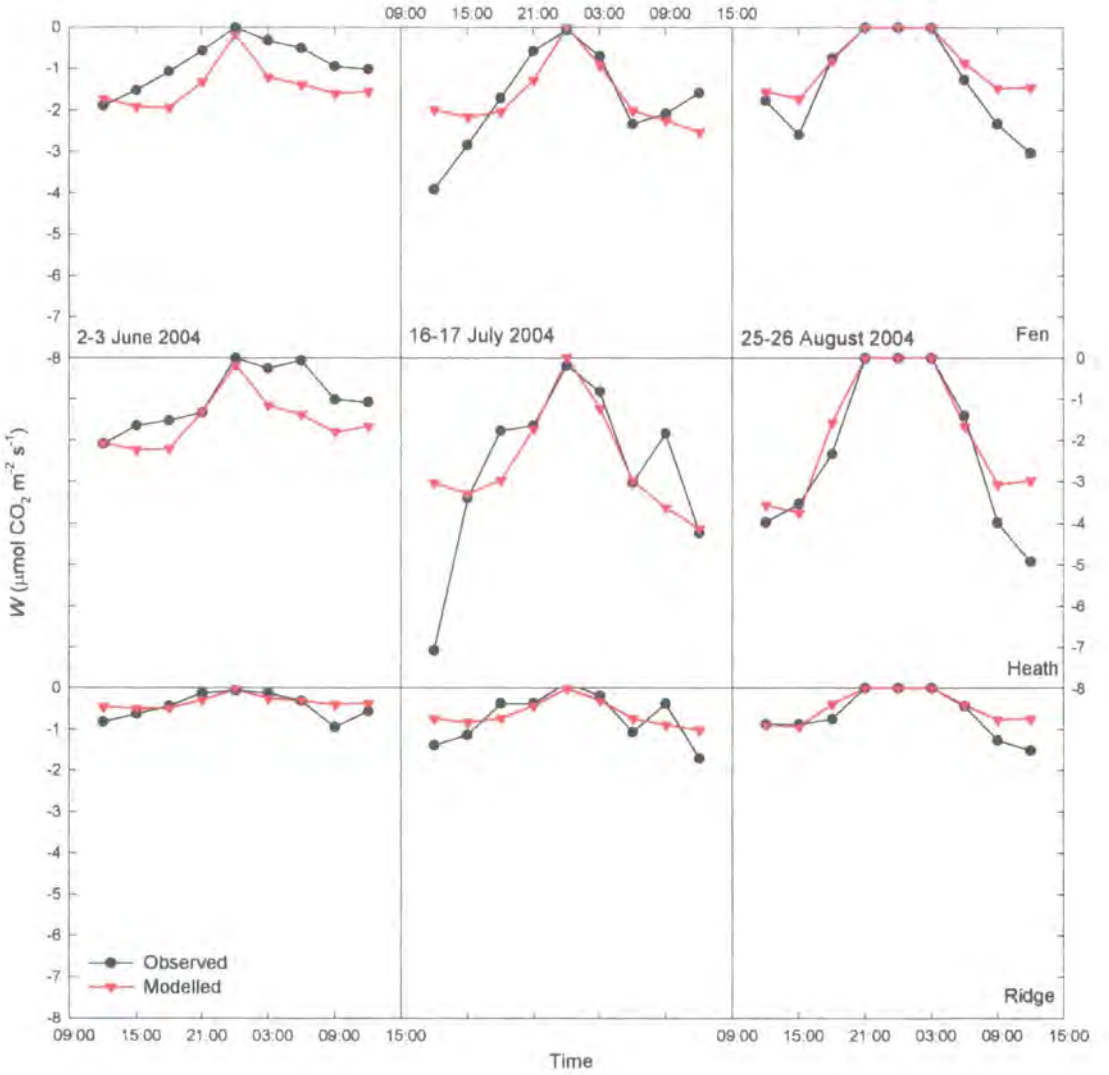

Figure 6-14: Modelled and observed values for photosynthesis in each of the three study communities for each of the three diel surveys.

6.2.5 *Net Ecosystem Carbon Dioxide Exchange*

Performance of the calibrated model for *NEE* in 2003 was found to be considerably poorer than it was for *R* or *W* (see Table 6-7, Figure 6-15 and Figure 6-16), with lower *d* values in nearly every instance and high *RMSE*, equivalent to 255%, 51% and 143% of $\overline{O}$ for the Fen, Heath and Ridge communities respectively (although this is partly due to the small values of $\overline{O}$ in each case), reflecting the combination of errors encountered in the prediction of both of the component fluxes.

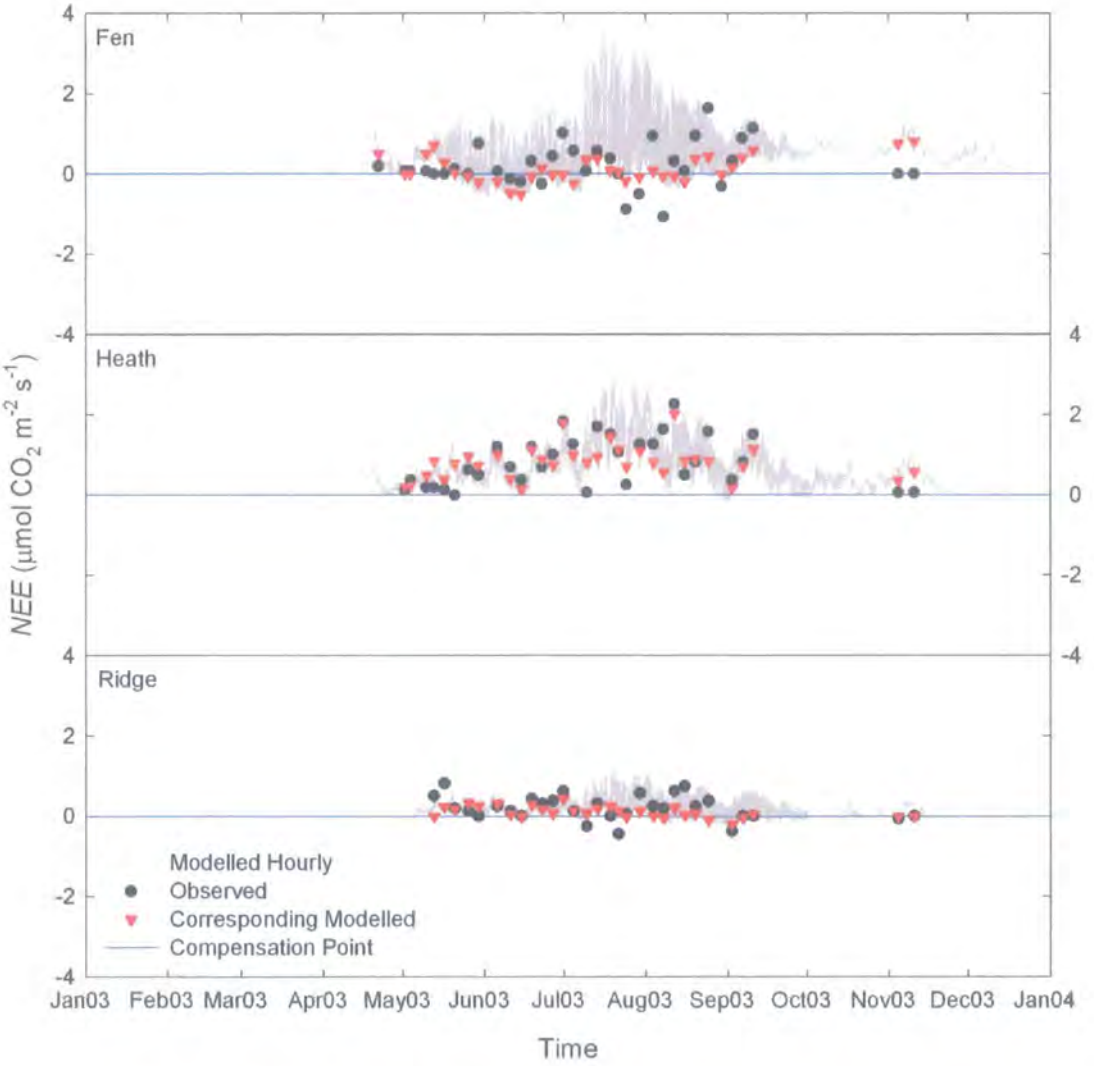

Figure 6-15: Modelled and observed values for net ecosystem CO_2 exchange in each of the three study communities, 2003.

Table 6-7: Model performance for net ecosystem CO_2 exchange (season data).

Community	2003		2004	
	d	RMSE	*d*	RMSE
Fen	0.52	0.56	0.53	0.60
Heath	0.82	0.42	0.66	0.77
Ridge	0.54	0.30	0.49	0.36

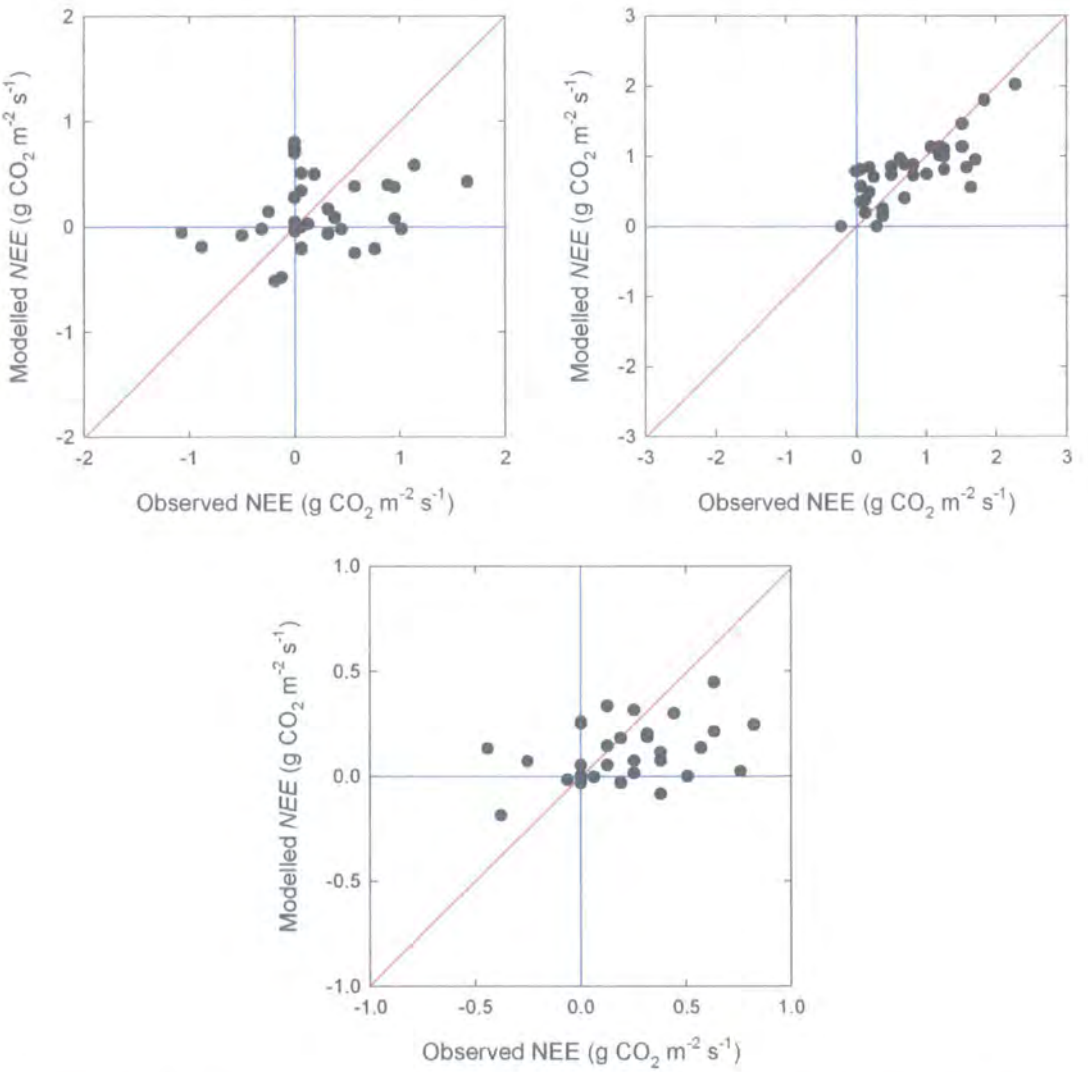

Figure 6-16: Observed vs. modelled net ecosystem CO_2 exchange for the Fen (top left), Heath (top right) and Ridge (bottom) communities, 2003. The red line indicates the position of a 1:1 relationship.

When tested against the 2004 season net ecosystem exchange data, performance of the model, as indicated by *d*, was found to stay the same for the Fen community, but became slightly worse for the Heath and the Ridge (see Table 6-7, Figure 6-17 and Figure 6-18). Values of RMSE became even higher in relation to $\overline{O}$, but again, this is largely an artefact of the observed NEE being so close to zero in each case.

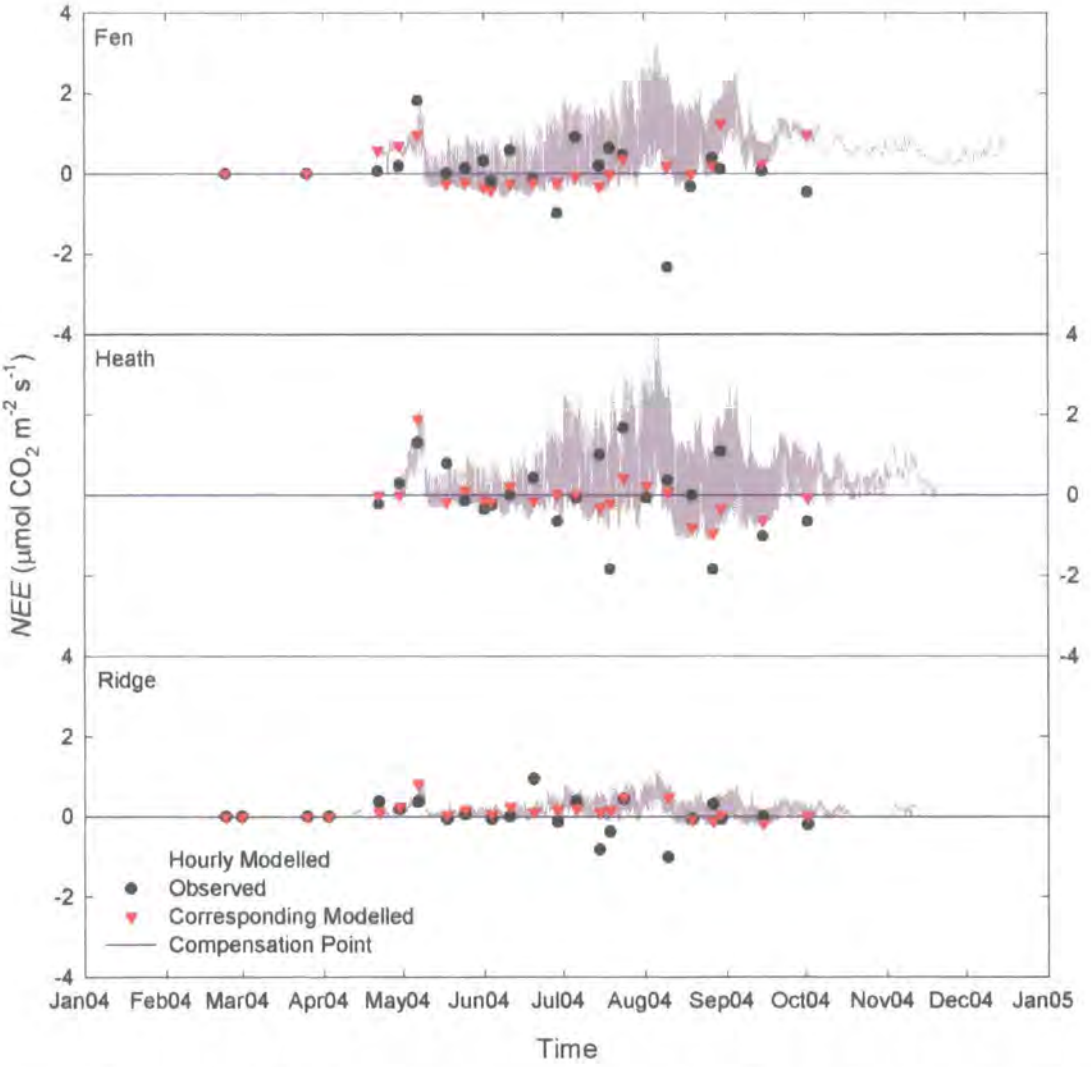

Figure 6-17: Modelled and observed values for net ecosystem CO_2 exchange in each of the three study communities, 2004.

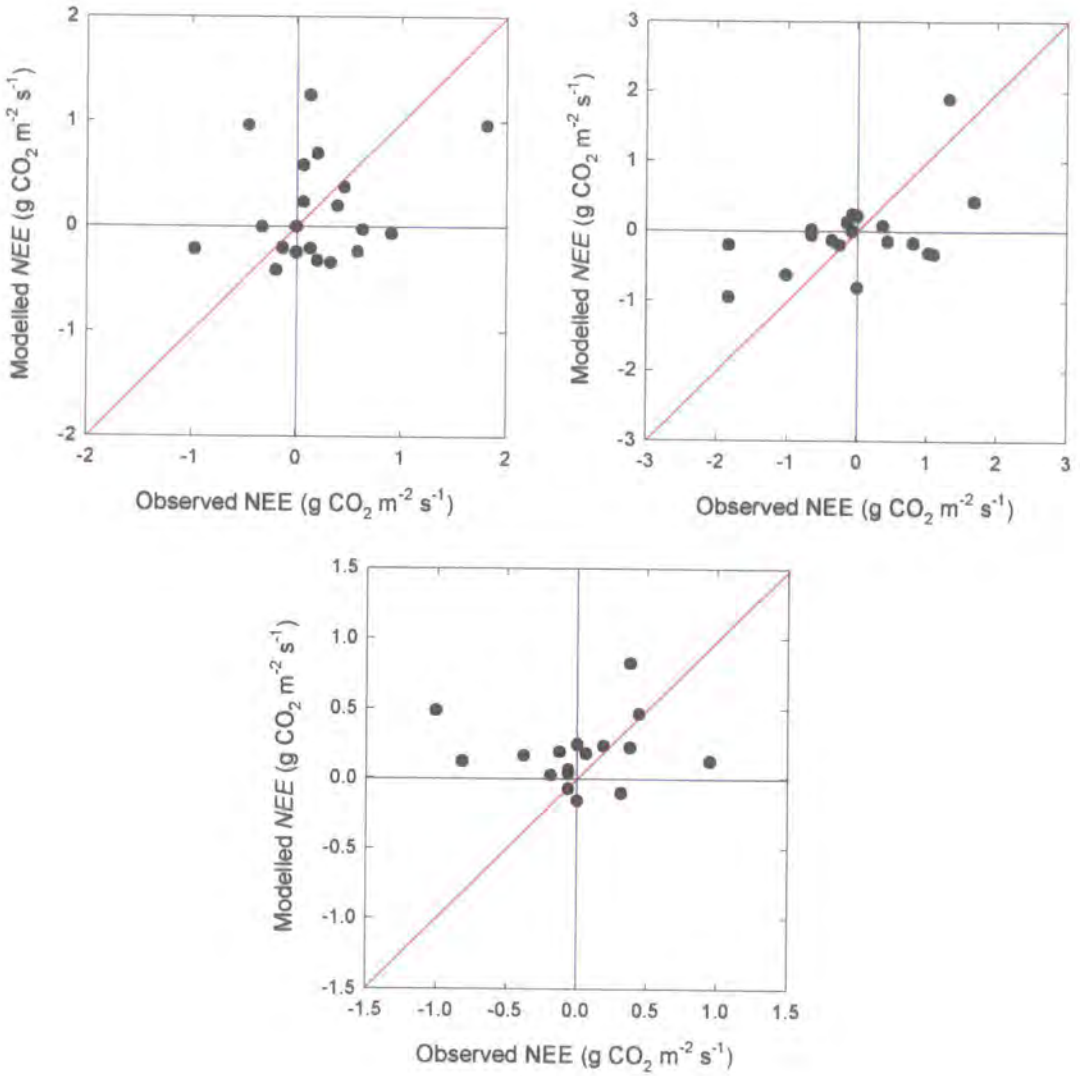

Figure 6-18: Observed vs. modelled net ecosystem CO_2 exchange for the Fen (top left), Heath (top right) and Ridge (bottom) communities, 2004. The red line indicates the position of a 1:1 relationship.

Performance of the model over the periods of the three diel flux surveys (see Table 6-8 and Figure 6-19) was generally as good, or better, than that observed for the season comparison, with better results in August than in June or July, reflecting the same trend observed for W. As with the season comparison, RMSE values were all very high in relation to $\overline{O}$, but as before, this is not necessarily a good indicator of model performance in this instance.

Table 6-8: Model performance for net ecosystem CO_2 exchange (diel data).

Community	2-3 June		16-17 July		25-26 August	
	d	RMSE	*d*	RMSE	*d*	RMSE
Fen	0.75	0.45	0.73	0.68	0.85	0.58
Heath	0.58	0.58	0.63	1.42	0.93	0.76
Ridge	0.56	0.25	0.45	0.59	0.91	0.21

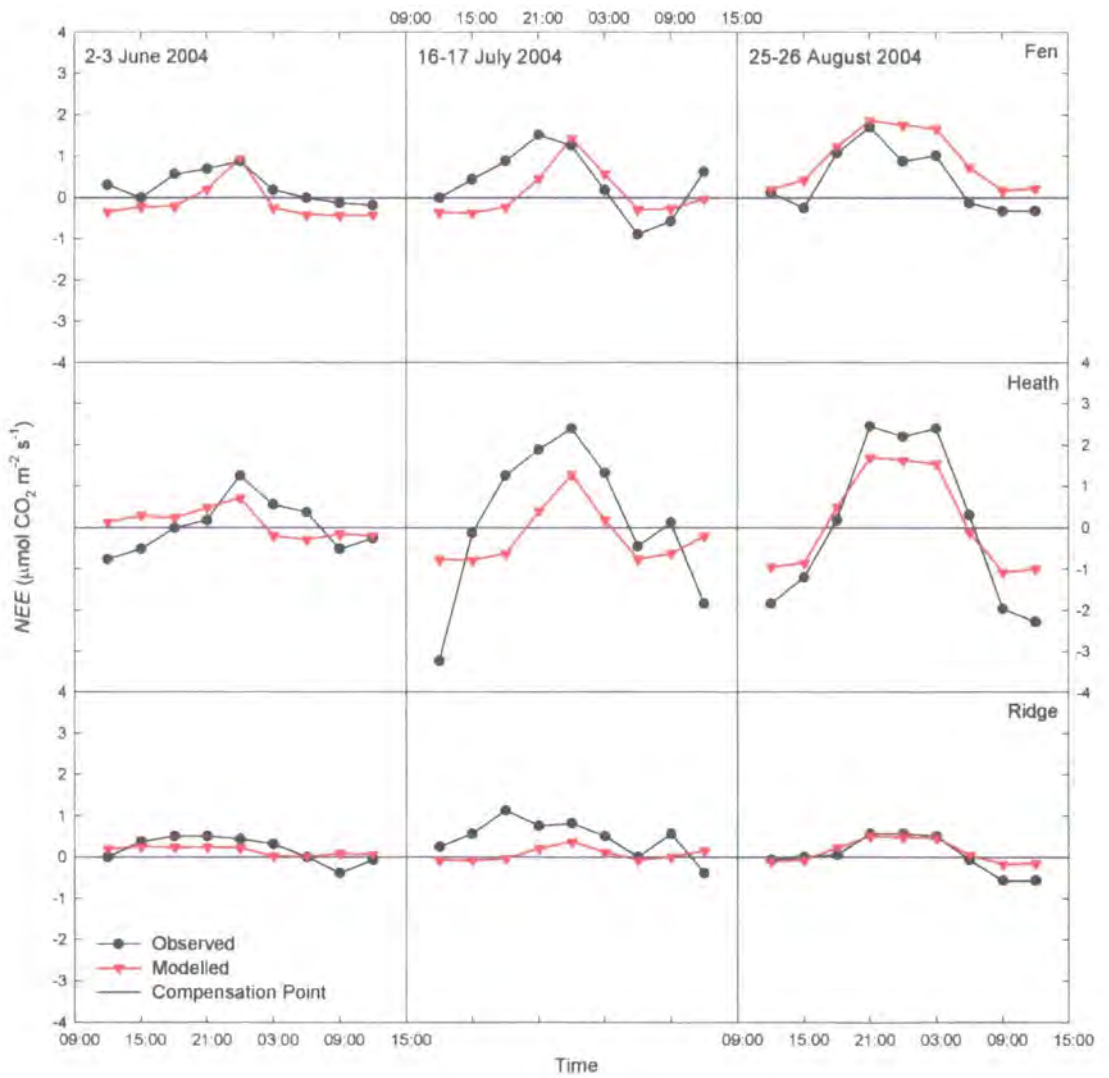

Figure 6-19: Modelled and observed values for net ecosystem CO_2 exchange in each of the three study communities for each of the three diel surveys.

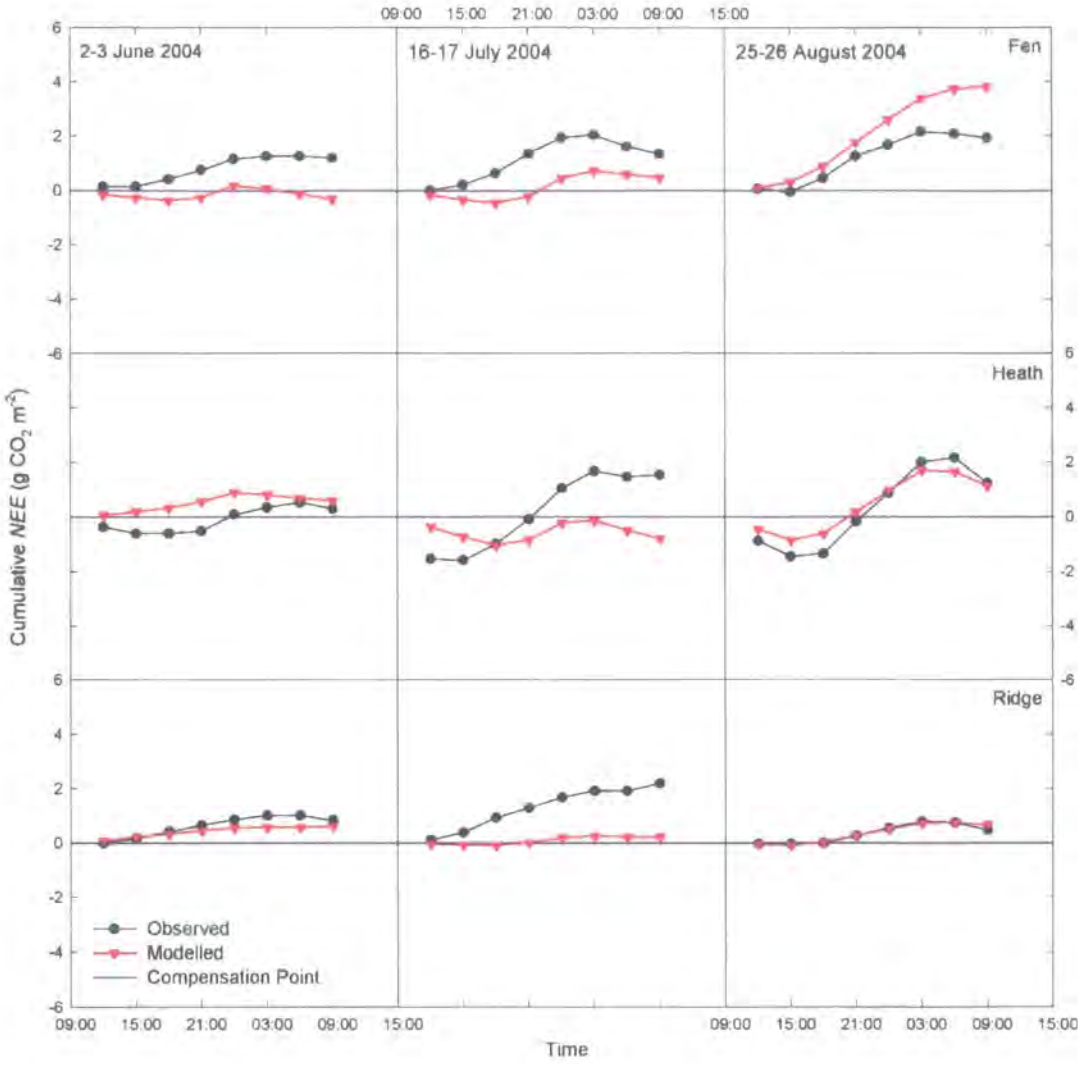

Figure 6-20: Modelled and observed values for cumulative net ecosystem carbon dioxide exchange in each of the three study communities for each of the three diel surveys.

Further insights into the performance of the model can be gained from a comparison of its outputs with the observed data over longer timescales. By summing the cumulative net ecosystem CO_2 exchange for each of the communities over each of the diel survey periods for instance, it is possible to assess the model's performance at a daily resolution, as opposed to the hourly resolution that has been worked with up until this point (see Figure 6-20). The accuracy of the modelled cumulative daily *NEE*, as indicated by the points to the far right of each plot, varies between communities and survey dates. For the June survey period, the model performs very well for the Heath and Ridge communities, but underestimates the daily efflux of the Fen community by 1.54 g CO_2 m^{-2}. For the July survey period, the model performs quite badly for all three communities, underestimating the daily

efflux by 0.88, 2.34 and 1.98 g CO_2 m^{-2} for the Fen, Heath and Ridge communities respectively. Performance improves again for August though, with accurate predictions for the Heath and Ridge communities, but an efflux overestimate of 1.87 g CO_2 m^{-2} for the Fen.

6.3 APPLICATION OF THE MODEL

6.3.1 Annual Carbon Balance

The three communities were all calculated to be net sources of CO_2 in both 2003 and 2004 (see Figure 6-21). The Fen community was estimated to be the strongest source overall, with a consistent net annual efflux of ~530 g CO_2 m^{-2} yr^{-1}. Like the Fen community, the Ridge was estimated to be a consistent, but smaller, annual

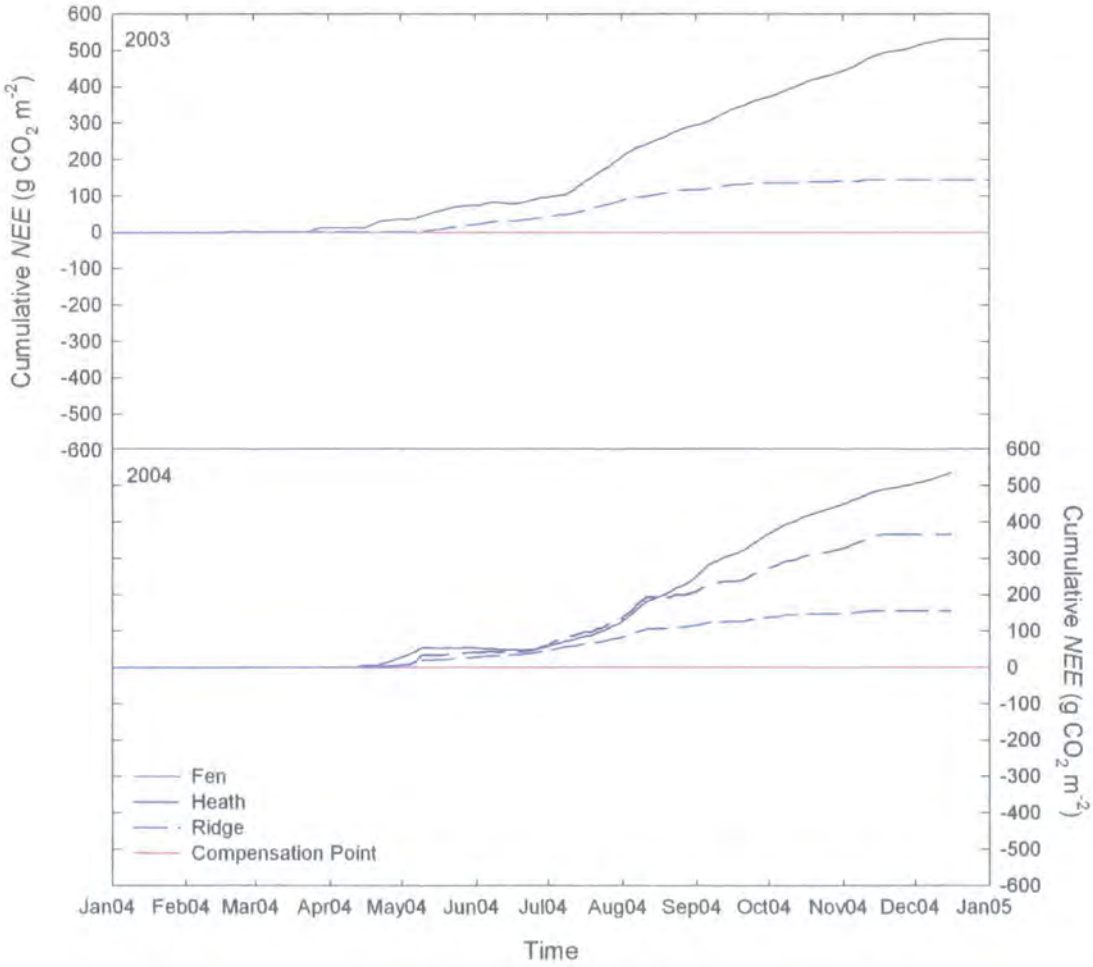

Figure 6-21: Modelled cumulative net ecosystem carbon dioxide exchange for the three study communities in 2003 and 2004. Values for the damaged 2003 Heath community are not shown.

source of ~145 g CO_2 m^{-2} yr^{-1}. The two years' estimates differed for the Heath community due to the restricted carbon assimilation resulting from the plant damage which occurred in 2003. Hence, the modelled Heath acted as a source of 589 g CO_2 m^{-2} in the first year and 366 g CO_2 m^{-2} the year after.

Unfortunately, the potential errors associated with these annual carbon balance estimates are large. Extrapolation of the *RMSE* values calculated for the season comparisons (Table 6-7) provides estimated errors in the region of ±772 in 2003 to 831 g CO_2 m^{-2} yr^{-1} in 2004 for the Fen community (equivalent to 146% and 157% of the modelled annual CO_2 balance for each year respectively), ±582 to 1065 g CO_2 m^{-2} yr^{-1} for the Heath (99% and 291%) and ±417 to 498 g CO_2 m^{-2} yr^{-1} for the Ridge (288% and 343%). However, extrapolation of these *RMSE* values is likely to overestimate the annual error as they are based on the half of the year when the majority of the CO_2 exchange occurs (the half of the year which is therefore most difficult to model). Assuming that there is virtually no exchange activity occurring during the half of the year when no observations were made and that the model is therefore accurate during this period, it may be acceptable to reduce the error values given above by as much as 50%. Although this considerably improves the confidence of the annual carbon balance estimates, the errors are still very large; in the case of the Heath community in 2004 and the Ridge in both years, the errors are still equivalent to more than 100% of the modelled cumulative CO_2 fluxes, casting doubt even on the direction of the net annual CO_2 exchange.

6.3.2 Sensitivity to Vegetation and Snow

Sensitivity of the model to its original parameter set has already been demonstrated by Harding et al. (2000), Huntingford et al. (2000) and Lloyd (2001). Here, analysis of model sensitivity has been performed only on those parameters that were introduced to the model for this study and/or those which are of particular relevance to the hypotheses in question; namely the vegetation cover parameters, C_{vasc}, C_{cryp}, C_D and C_{Ev}, the phenology parameters, g, S and s, and the timing of snow melt, as given by *SI*. This will hopefully provide some insight as to the importance of these factors in real Low Arctic ecosystems. In each case, the parameters were altered by ±50% (where possible), with the exceptions of S and *SI*, which were both altered by ±30 days, to see what influence this would have on the 2004 annual CO_2 balance of the three study communities.

Lloyd (2001) reported a large influence of the vegetation cover parameters, C_{vasc} and C_{cryp}, upon *NEE* outputs for his High Arctic polar semi-desert site. Similarly in this study, varying C_{vasc} by 50% was found to alter the 2004 total *NEE* by 54%, 115% and 67% for the Fen, Heath and Ridge communities respectively, with increased source strength associated with decreased vascular plant cover and *vice versa*. Comparable variations in C_{cryp} on the other hand, were only observed to have a very minor influence on annual *NEE*.

The proportions of the vascular plant cover which are deciduous and evergreen, given by C_D and C_{Ev} respectively, determine the extent of the role played by the model's new phenology component. Although less influential than the fundamental vegetation parameter, C_{vasc}, 50% variations in C_D and C_{Ev} were still found to bring about annual *NEE* changes of 13%, 29% and 19% for the Fen, Heath and Ridge communities respectively, with increased source strength associated with increased deciduous cover (and decreased evergreen cover accordingly).

Of the phenology component parameters, the model was generally found to be more sensitive to variations in the rate of leaf area expansion, *g*, than the rate of senescence, *s*. For the Heath and Ridge communities, a 50% increase in *g* reduced annual net CO_2 efflux by 14% and 10% respectively, while reducing the value of the parameter by the same amount increased net efflux by 31% and 24%. In comparison, analogous variations in *s* resulted in increases of 5% and 2%, and decreases of 8% and 2% for the Heath and Ridge communities respectively. For the Fen community, *s* was actually slightly more influential than *g*, causing annual *NEE* changes of -9% and +5% as opposed to +8% and -3%. In all cases however, altering the variables so as to lengthen the period of maximal leaf area, resulted in reduced net CO_2 efflux and *vice versa*. As is true of the remaining phenology parameter, *S*, which determines the timing of senescence initiation. Delaying this event by 30 days was found to reduce annual net CO_2 efflux by 13%, 12% and 5% for the Fen Heath and Ridge communities respectively. Advancing senescence initiation by 30 days however, was found to have a greater influence; increasing net efflux by 23%, 26% and 14%.

Figure 6-22 displays the modelled relationship between the timing of snow melt and total annual *NEE*. Delaying snow release by 30 days was only observed to have a minor influence, bringing about respective reductions in CO_2 efflux of 1% and 2% for the Fen and Ridge communities, but increasing efflux by 4% for the

Heath. Advancing snow release by 30 days had virtually no effect at all. As can be seen in Figure 6-22 however, further decreases in the length of the growing season by delaying the date of snow release eventually results in a decline in annual *NEE* towards the compensation point.

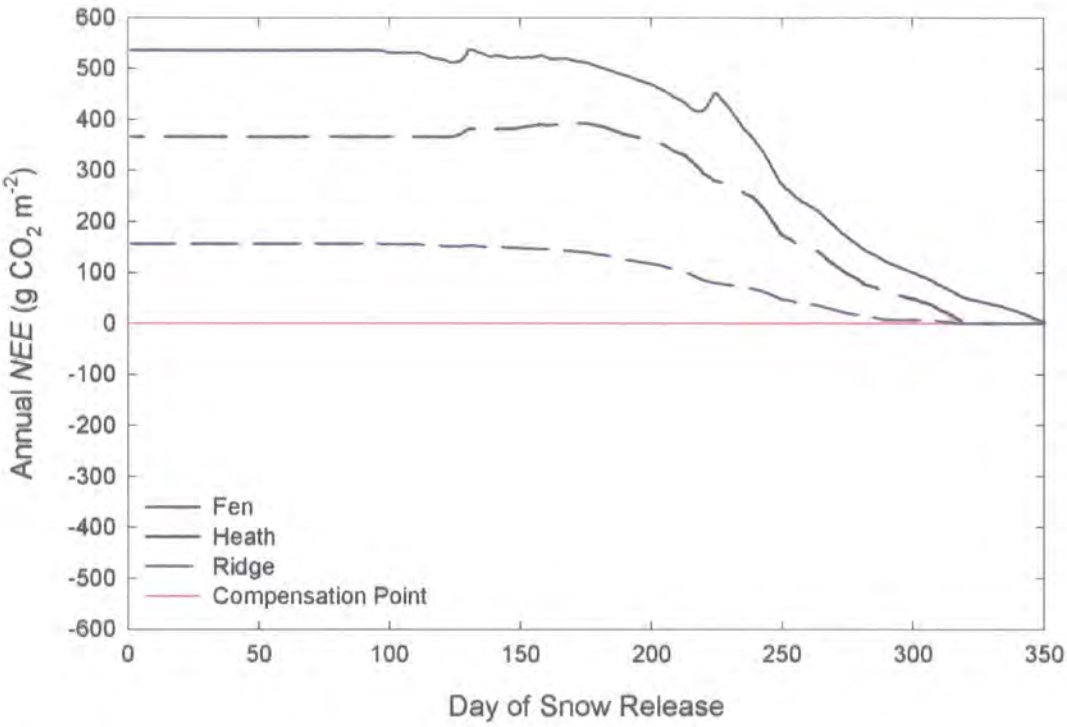

Figure 6-22: The modelled relationship between the timing of snow melt and annual net carbon dioxide exchange for the three study communities in 2004.

CHAPTER 7: DISCUSSION

7.1 ABIOTIC PARAMETERS

Snow depth and duration were successfully manipulated for both the field and the monolith experiment. In each case, the magnitude of the perturbations were generally in excess of any changes likely to occur as a result of climatic warming over the next century (Sælthun & Barkved 2003, Kattsov et al. In Press), but nonetheless provide an appropriate degree of contrast for highlighting the significance of snow cover in these Low Arctic tundra plant communities.

Both experiments demonstrated the well known insulative influence of snow depth and duration on soil temperature (see section 1.1). In the field experiment, winter soil temperatures were higher where the snow cover had been increased, but temperatures also remained cooler for longer in the spring. Summer soil temperatures on the other hand, appeared to be influenced more by other factors such as vegetation and hydrology, as the only observed significant differences were between communities. The results of the monolith experiment complement these findings. Winter soil temperatures were warmer where snow depth was increased and coolest where there was no snow at all. Again, where the duration of snow cover was prolonged, the warming of the soil in the spring lagged accordingly. In the monolith experiment, the only difference in summer soil temperatures was between the 'site control' monoliths (at the fieldsite) and those at the research station, where the 'site controls' were consistently cooler. This is no doubt a result of the 400 m altitude difference between the two locations.

Despite the potentially large differences in snow water input that would have been associated with the observed contrasts in experimental snow cover, snow-free season soil moisture values did not differ significantly between treatments in either the field or monolith experiment. This is probably due to the fact that snow melt occurred before the soil had thawed sufficiently to absorb the available moisture. As was similarly observed in a study of high mountain catchments in central Norway (Löffler 2005), increases in water inputs at this time would have resulted in greater surface runoff to more topographically depressed areas, as opposed to local increases in soil moisture. As with soil temperature, summer soil moisture appeared to be influenced more by factors other than snow, such as vegetation and topography, as

the only significant differences were observed between communities in the field experiment.

The main influence of short-term changes in snow cover on growing season conditions appears to be via their effect on when the season begins, which, in terms of factors such as PAR, determines both the intensity and the duration of availability. Delays in snow melt in the region of those observed in the '+snow' treatments of the field and monolith experiments for instance, were found to reduce total available solar radiation by up to 25% over the course of the year, while the advances in snow melt increased the annual total by about 15%. This sensitivity to snow melt timing is a result of the high levels of insolation to which the Low Arctic is exposed in late spring/early summer. Air temperatures on the other hand, are not typically very warm at this time; therefore, greater changes in the timing of snow release are required to influence the accretion of GDDs. Indeed, the only difference in annual GDD accumulation likely to be of any consequence was that observed between the 'site control' monoliths and those at the research station; yet this was more a result of the difference in altitude than any discrepancy in snow cover.

7.2 PLANT PHENOLOGY

In accordance with previous snow augmentation studies (Weaver & Collins 1977, Rixen et al. 2001, Rixen et al. 2003), significant delays in plant phenological development in response to increased snow cover duration were observed in both the field and monolith experiments. Both vegetative and reproductive phenology were affected, although the greatest delays were generally restricted to the earlier phenophases. Very few significant treatment effects were observed in phases occurring more than one month after the last of the snow had melted from the plots (the end of June and the end of May for the field and monolith experiments respectively), indicating a telescoping of phenological development in response to the '+snow' manipulations, as reported by Walker et al. (1999). It may be the case that such accelerated development is a positive response, reflecting the more favourable growing conditions encountered by plants emerging from the snow later in the year. It is also possible however, that such increases in developmental speed put a greater strain on the plants' already limited resources, rendering such a strategy

infeasible and perhaps, detrimental, as a long-term response to prolonged snow cover duration.

Despite the observed phenological differences, analysis of the fixed point photographs revealed no conspicuous divergences in seasonal greenness trends at the community level in response to the '+snow' manipulation. It may be that the responses observed in the study species are offset by different responses from other species; where the vegetation is largely evergreen for instance, as in the Heath community, changes in the timing of leaf bud burst for a deciduous species such as *B. nana* are likely to be masked by the dominating contribution to image greenness made by *E. hermaphroditum*. Similarly, in the Fen and Ridge communities, greenness trends are likely to be masked to some extent by the influence of dead leaf material and bare ground (each of which cover a considerable proportion of the surface area in these communities). Such trend-masking may also explain the disparity that has been reported between ground-based observations of *B. pubescens* ssp. *tortuosa* phenology, which show changes in the timing of leaf bud burst, and satellite observations, which show no such trend (Karlsson et al. 2003). This highlights the importance of the spatial scale at which phenological observations are made.

Advancement of snow melt, as implemented in the monolith experiment, was found to have less of an impact on plant phenology than prolonging snow cover duration, perhaps partly due to the fact that the '+melt' manipulation only advanced snow melt by a few days compared to the 'control'. As before, any advancement in early season development associated with earlier snow melt was soon countered by the telescoped progression of those individuals released from the snow later in the year. Without the concurrent increase in air/soil temperature factored into previous early melt experiments (Oberbauer et al. 1998, Price & Waser 1998, Starr et al. 2000, Dunne et al. 2003), advanced snow release therefore appears to provide the plants with little advantage.

Delaying the arrival of snow cover in the autumn had no discernable effect on plant phenology. However, when snow cover was prevented all winter, reproductive phenology was found to be retarded in some cases. This concurs with the findings of Inouye & McGuire (1991) and may similarly have been a direct result of winter frost damage incurred by preformed buds in the absence of adequate insulation; the reproductive ecology of Arctic plant species can be very susceptible

to specific climatic events occurring in the winter and spring (Tolvanen 1997, Aerts et al. 2004). It could alternatively be an indication of reduced nutrient availability resulting from a temperature induced perturbation of soil microbial dynamics. Previous research on Subarctic tundra heath monoliths carried out by Grogan et al. (2004) has demonstrated the strong influence of freeze-thaw regime on the amount, form and timing of soil N and organic C supplies.

Although a slight deviation from the central focus of this study, the contrast observed in the phenologies of 'site control' monoliths at the fieldsite and all the other treatments at the research station, is highly indicative of the importance of growing season conditions in the regulation of plant development. Similar to the delays in phenology associated with increasing altitude observed by Lévesque et al. (1997) in the Canadian High Arctic, most phenophases occurred significantly later at the fieldsite than at the research station. This was most probably a result of the pronounced difference in summer temperatures observed between the two locations. As reported by Jones et al. (1997) and Arft et al. (1999) however, foliar senescence does not appear to be affected by this altitude/temperature difference. Combined with the above mentioned observation that late season phenology is generally unrelated to the timing of snow release, it would seem that the timing of senescence is regulated predominantly by factors other than growth period or temperature (at least for the selected study species).

Despite general similarities, considerable variability was observed in the responses of the different study species to the manipulations, reflecting the differential sensitivity of Arctic plants to environmental cues reported by Sørensen (1941) and Molau et al. (2005). The degree to which a particular species was affected appeared to be largely dependent upon the "natural" distribution of its phenological development throughout the growing season. The reproductive phenologies of later flowering species such as *D. octopetala* and *V. vitis-idaea* for example, exhibited much less of a response to delays in snow release than those of early flowering species such as *A. polifolia*, just as some were able to take more advantage of early snow release than others. If such interspecific variability was to manifest itself in the performance and hence, the competitive ability of these plants, this could provide a powerful mechanism by which snow cover could influence community composition and, in turn, ecosystem function.

As well as varying between species, phenological responses to the snow manipulations were found, in a number of cases, to be dependent on the plant community. The effect of community type probably reflects the influence of one or more of a number of spatially heterogeneous environmental factors such as the prevailing (non-manipulated) snow regime, soil temperature, hydrology, nutrient availability and plant competitive pressure, as well as potential genetic differences between community specific ecotypes. In areas characterised by high environmental heterogeneity, no single set of phenological traits is optimally adapted, thus promoting the co-occurrence of multiple adaptive strategies (Jackson & Bliss 1984). These are likely to be the same factors responsible for the natural inter-community variability observed in the phenologies of a number of the study species.

In a number of instances, phenological responses to snow manipulation were also found to be dependent on the year. This probably reflects natural interannual variability in the environmental factors mentioned above, which could also account for the observations of natural variations in phenology between years. Research carried out by van Wijk et al. (2003b) has already demonstrated how interannual variability in the leaf bud burst phenology of *B. nana* can be predicted with a high degree of accuracy according to the timing of soil thaw at 10 cm. However, the divergences may also be indicative of a temporal shift in plant response; the greater delays observed for *B. nana* in the field experiment in 2004 for example, may have been a result of a reduced ability to accelerate its development, having diminished its resources through acceleration in 2003 (see above).

7.3 PLANT PERFORMANCE

7.3.1 Vegetative Growth

Significant increases in stem growth in response to two years of the '+snow' manipulations were observed for both of the species in which this parameter was monitored. However, these increases were community-dependent, with the evergreen shrub, *E. hermaphroditum*, only affected in the Ridge community, and the deciduous shrub, *V. uliginosum*, only affected in the Heath. These results concur with those of Scott & Rouse (1995), who found that the growth of moisture-tolerant species such as *V. uliginosum* responded positively to increases in winter snow

cover, while non-tolerant species declined, and Wahren et al. (2005), who also reported species/community dependent responses to artificial snow augmentation. Although it is not possible to identify the exact mechanisms responsible for the observed responses, potential candidates include increased protection of apical buds over the winter and spring, increases in nutrient availability due to warmer winter soil temperatures and, perhaps, etiolation as a result of reduced light levels in the spring. Contrary to the indications of the previous studies, the results of the soil moisture surveys presented here suggest that changes in hydrological regime are unlikely to have played a role. However, the influence exerted by the snow manipulations would no doubt have depended upon the prevailing snow regime which, along with other spatially heterogeneous factors such as soil temperature, soil moisture, solar radiation and perhaps, ecotypic diversity, would also have contributed towards the natural variability in stem growth observed between the three study communities, variability which has, over time, determined the nature of the structural and compositional characteristics by which the communities are distinguished.

Despite the potential for taller, less branched morphologies offered by a deeper, more protective snow cover, the effect of the '+snow' manipulations on stem architecture via branching was less pronounced than it was for growth. Although one significant decline in branch formation was observed with increased snow cover, even after correction for interannual variability there was still a high degree of apparently stochastic variability between the control and '+snow plots', both before and after the start of the experiment. Combined with the observation that the frequency of branch formation differed significantly between the three study communities, this could be interpreted as evidence that regulation of branching in these species is predominantly autonomous, and that each of the communities is inhabited by genetically distinct ecotypes, presumably selected by a combination of pressures from both the abiotic environment and plant-plant interactions over a time scale well beyond the scope of this study. On the other hand, the apparent randomness may reflect patterns in herbivory intensity (Batzli 1975).

The manipulation responses of the various leaf parameters that were monitored for the selected study species were found to be highly individualistic. *B. nana* leaves were not affected by the '+snow' manipulation except for a decrease in nitrogen content observed in the Fen community. *V. uliginosum* leaves on the other

hand, increased in size and weight in response to snow addition, but only in the Heath community. Their nitrogen content also decreased in the Fen and Heath communities, but increased in the Ridge. Interestingly, the exact opposite leaf nitrogen response was observed for *E. hermaphroditum* (no size or weight data were collected). This suggests that plant growth form may be an important factor in determining the nature of snow-ecosystem interactions, as, again, is the type of community involved. In each case the observed changes in leaf nitrogen contents are likely to reflect a complex combination of perturbations to factors affecting nitrogen availability (microbial activity, snow inputs, leaching rates) and utilisation (plant allocation, growth rates), as was probably the case in previous studies which have reported changes in leaf chemical composition in association with snow augmentation (Henry & Molau 1997, Walsh et al. 1997, Welker et al. 2005). Leaf phosphorus concentrations were not found to be as sensitive to changes in snow cover in any of the species for which they were measured. It is important to note however, that, as no measurements were made of the number of leaves produced, it remains to be seen how the observed leaf responses mentioned above correspond with the overall response at the level of the individual plant.

7.3.2 Reproductive Output

Of the three species included in the flower survey, only *A. polifolia* was significantly affected by the snow manipulation. The observed reduction in flowering after two years of increased snow cover is congruent with the findings of Kudo (1991, 1992), who reported similar trends in natural alpine snow gradients for a number of species. In this case, the decrease in flowering could be a response to either the current year's delayed snow release, constriction of the previous growing season, or perhaps a combination of the two. Whether the response reflects a decline in plant resources or a shift in life history strategy (or both) is also unknown, but either way, the species specific nature of the response indicates another pathway by which snow cover may influence community composition; although the efficacy of this pathway would ultimately depend both on the relationship between flower number and reproductive success and the potential for seedling establishment as opposed to vegetative propagation. Indeed, the occurrence of significantly greater flower production in the Ridge community than in the other communities for *B. nana* and *V. uliginosum* could be interpreted as an indication that greater sexual reproduction is a more favoured

strategy in this sparsely vegetated environment and that different ecotypes have adapted accordingly. Of course, it could also be a direct response to the divergent abiotic factors that characterise the three study communities.

Although there were no significant differences between treatments for fruit production (due largely to high within-treatment variability), the general trend in the data follows that observed for flowering, with fewer *A. polifolia* fruits produced in the '+snow' plots. This is likely to be a direct result of the observed reduction in flowering, but may also potentially reflect reduced pollinator activity around the time of flowering in the delayed plots (see section 2.2). Similar to the trend in flowering, fruit production by *B. nana* and *E. hermaphroditum* was far greater in the Ridge community than in the Fen or Heath. Again, this is due to a combination of unknown genetic and/or environmental factors as discussed above.

Despite the absence of any significant treatment effects on the quantity of fruits produced, fruit quality does appear to have been affected; although once more, the response was found to be species-specific. While no differences were observed for *E. hermaphroditum* (between treatments or communities), in the one community in which it was possible to conduct a survey (the Ridge), *V. uliginosum* berries were found to weigh approximately half as much as the controls (dry weight) where the snow cover had been manipulated. Although it is not possible to be sure without removing the seeds from the berries and weighing them separately, the observed decrease in berry weight could, at least partly, be due to a decrease in seed weight similar to that reported by Galen & Stanton (1991, 1993). The weight reduction was probably caused by constriction of the window of opportunity available for berry/seed development, as well perhaps, as the diversion of resources to the acceleration of phenology in general. Assuming that berry dry weight is a good indicator of seed weight, and that this is positively correlated with germination success, this may provide yet another pathway by which snow cover can influence community composition; although such an influence could potentially be confounded by concomitant modification of the environment in which the seeds are dispersed.

7.4 CARBON DIOXIDE EXCHANGE

7.4.1 Experiments

Although initial analysis of the CO_2 exchange data (by repeated measures ANOVA) revealed no overall significant differences between the 'control' and '+snow' treatments in any of the field communities or the monoliths, analysis of the linear relationships between the two treatments did highlight a number of differences. In both the Fen and the Ridge communities, ER and GPP were found to be proportionally lower after snow augmentation (but only in 2004 in the Fen). Similarly, in the monolith experiment, ER was found to be proportionally lower in the '+snow' treatment than in the '+melt' (although neither differed significantly from the 'control'). While the cause of these proportional reductions is not clear, such responses may be linked to possible restrictions of above and belowground community development imposed by the delayed onset of biological activity in the spring (see section 7.2). On the other hand, they may be a result of changes in the rates of cycling of carbon and nutrients through the soil due to greater winter biological activity associated with increased insulation (see section 1.1 and section 2.2); after all, the results of this and previous studies demonstrate how snow augmentation can affect leaf nitrogen concentration (see section 7.3). Analysis of the linear relationships between the 'control' and '+snow' data also revealed some proportional and absolute differences in NEE. However, the relationships were generally poorer than those for ER and GPP, making the trends more spurious. In contrast, previous studies by Jones et al. (1998) and Welker et al. (2000) reported considerable reductions in net CO_2 efflux in response to short-term snow augmentation.

In the monolith experiment, the only other treatments which were found to have a significant impact on growing season CO_2 exchange (by repeated measures ANOVA and analysis of the linear relationships) were '0snow' and 'site control'. In both cases, ER and GPP were lower (closer to zero) than in the 'control', with no overall change in NEE. The difference between the monoliths at the fieldsite and those at the research station is most probably a result of direct growing season temperature effects on plant/microbe metabolism and possibly also indirect temperature effects via changes in nutrient availability. This response is similar to the increases in carbon turnover with warming reported by Johnson et al. (1996),

Hobbie & Chapin (1998) and Marchand et al. (2004a). The response to the '0snow' manipulation is also likely to reflect differences in temperature; this time, differences in winter temperatures that resulted from the lack of insulation. As with the observed phenological delays (see section 7.2), changes in nutrient availability induced by the severe freeze-thaw regime and frost damage to plants are likely to have been important factors in this instance. Although no quantified observations of frost damage were made, the plants in the '0snow' monoliths did appear to be in poorer health (less green) than the plants in the other treatments (personal observation).

As well as the manipulations, significant differences in CO_2 exchange were also identified between the three study communities at the fieldsite (by both of the statistical methods employed), with generally greater ER and GPP in the Fen and Heath communities than in the Ridge, as well as differences in the timing of the seasonal trend in this activity. One of the most obvious differences between the Fen/Heath and Ridge communities to which these differences in carbon turnover may be attributed is biomass (amount, type and structure); both above and belowground, the Ridge community contains very little live plant/microbial material compared to the Fen and the Heath. While this is likely to account for much of the discrepancy in carbon turnover between the communities, it is difficult to uncouple the role of biomass from the abiotic environmental factors such as snow cover and hydrological regime, which, in the long term, interact with the biotic components of the ecosystem to determine their composition and structure. Despite the observed differences in carbon turnover, the only differences in NEE were between the Fen and the Heath in 2003 (more negative in the Fen), and between the Heath and the Ridge in 2004 (more negative in the Ridge). The variable role of the Heath community between years is no doubt a result of the vegetation damage caused by the insertion of the flux measurement collars in 2003 and the switch to non-damaging collars in 2004.

7.4.2 Modelling

The performance of the CO_2 exchange model was found to differ between variables (ER, GPP and NEE), communities, years and timescales. Of the three variables, performance was poorest for NEE, due to the combination of errors arising in the

estimation of both ER and GPP. These errors may have originated from a number of different sources.

Firstly, there may be inaccuracies in the observation data used to calibrate and test the model; the measurement of CO_2 exchange in the field by the closed chamber technique is not 100% accurate (Freijer & Bouten 1991, Lund et al. 1999, Longdoz et al. 2000, Davidson et al. 2002, Widén & Lindroth 2003). Although every effort was taken to minimise errors in the observation data, a small but unknown degree of non-systematic inaccuracy must be assumed due to the potentially confounding effects of soil air spaces, wind/temperature induced pressure differentials and turbulence perturbations within the chamber.

Secondly, there may be inaccuracies in the driving parameter data due to spatial and temporal discrepancies, as well as any inadequacies in the instrumentation/methodology that was employed. In the case of ER for instance, some portion of the error may be attributable to the fact that neither soil temperature nor moisture were measured at the actual location being modelled in any of the communities. Manual observations of soil temperature at the Ridge flux collars for example, were found to be far more variable, with a much greater range, than the automatically measured temperatures. For GPP, there is the added potential error associated with the difference in timescale between the time over which CO_2 flux observations were made (two minutes) and the time over which the driving parameters are averaged for the model's hourly time-steps, as incoming shortwave radiation levels may differ greatly between the two timescales on days with patchy cloud cover.

Thirdly, the model's representation of the underlying physical processes may be flawed. Even if it were possible to obtain perfect data to calibrate, drive and test it, if the model's structure is oversimplified or wrong in some way, so will be its output.

Although it is not possible to quantify to what extent each of the above sources has contributed to the errors observed in this study, it is inevitable that observational inaccuracies have occurred, both for the CO_2 fluxes and the driving data. Therefore, the model's representation of the underlying processes may actually be better than its performance suggests. Indeed, although Lloyd (2001) applied the model to a different, much less active system, he demonstrated that it is capable of effectively simulating net ecosystem CO_2 exchange. Of the two sources of

observational error, inaccuracies in the measurement of CO_2 flux are likely to have been less influential than inaccuracies in the measurement of the driving variables; this highlights both the importance of spatial heterogeneity in determining NEE and the necessity for the accurate measurement of driving variables as close to the location being modelled as possible.

The model estimated that the three study communities were all net annual sources of CO_2 to the atmosphere in both 2003 and 2004. The greatest annual effluxes occurred in the Fen community and smallest in the Ridge, with little sign of natural interannual variability in either. The source strength of the Heath community was intermediate to the Fen and Ridge in 2004 (the only year for which a reliable Heath estimate was obtained, due to the vegetation damage that occurred in 2003). All of the model estimates lie within the range of values reported by previous studies of annual Arctic tundra CO_2 balance (see section 2.3). Analysis of the Abisko Scientific Research Station meteorological record shows that, in terms of temperature, both years were ~1°C above the 1971-2000 average, but still well within the normal range of variability, suggesting that the estimated fluxes for these two years are unlikely to be an artefact of atypical weather conditions (although other meteorological/environmental variables for which there is no long-term record at the fieldsite, could possibly have differed from the norm). In addition, estimates of soil carbon content for the three study communities (up to 50 kg C m^{-2} in the Heath) (P. Wookey Personal Communication) suggest that there is sufficient carbon to fuel such CO_2 effluxes for many decades. Given the magnitude of the potential errors involved however, the actual fluxes may have been considerably smaller, and in the case of the Heath and Ridge communities, may actually have been in the opposite direction.

It is also important to note that the three patches of tundra modelled here are not necessarily good representatives of the three communities to which they belong. The model was found to be very sensitive to variations in vegetation cover, both in terms of the area occupied by vascular plants as opposed to cryptogams or bare ground, and to a lesser extent, the proportion of the vascular plants that were deciduous as opposed to evergreen. These parameters varied greatly within each of the different communities (personal observation). It is therefore quite likely that the average community values differed considerably from those used to run the model here; if anything, average community vegetation cover was probably greater than the

vegetation cover within the flux measurement collars. If this were so, actual rates of community CO_2 assimilation would have been higher and source strengths, weaker. Vegetation cover parameters were found to be a great source of uncertainty in an attempt to model the GPP of an Arctic watershed in Alaska, due to the high degree of heterogeneity in the landscape and the high sensitivity of GPP to changes in vegetation cover at the low levels found in the Arctic (Williams et al. 2001).

The sensitivity of the model to its phenological parameters demonstrates the importance of plant phenology in the determination of Low Arctic tundra ecosystem carbon balance. This concurs with the observations of Harazono et al. (2003), who reported increased CO_2 assimilation in an Alaskan wet sedge tundra in association with earlier vegetation development. Rates of leaf area expansion tended to be more influential than senescence rates, unless senescence was initiated earlier in the season, as in the Fen community. This reflects the superior conditions for photosynthesis at the beginning of the snow-free season compared with those at the end. For both leaf area expansion and senescence, changes that extended the period of maximum leaf area had less of an effect than changes that reduced the period by the same magnitude, indicating that the vegetative phenological strategies of these plants are presently close to the optimum for maximisation of carbon assimilation.

In contrast, the model was found to be insensitive to the timing of snow melt unless it was delayed by more than around three months, after which the estimated annual CO_2 exchange rates steadily declined with increased snow cover duration. This is contrary to the findings of Aurela et al. (2004), who found that natural variability in the timing of snow melt controlled the annual CO_2 balance of a Subarctic fen in Finland, and model estimates from White et al. (1999), which indicate that the NEE of cold environments is particularly sensitive to changes in growing season length. In this study however, snow melt date was manipulated in an extremely simplified and somewhat unrealistic manner, especially in the case of snow melt advancement. This is due to the fact that when the model is manipulated in this way it does not take into account a number of important factors such as the energy balance (in reality, early snow release is likely to lead to advanced soil/air warming in the spring), moisture availability, nutrient cycling and the occurrence of frost damage. Consequentially, all that can really be inferred from this exercise in respect to snow cover is that moderate delays in snow melt timing have little effect

on annual carbon balance via their influence on the timing of the start of the growing season alone.

7.5 SUMMARY AND CONCLUSION

In both experiments, severe manipulations of winter snow depth and duration were found to affect winter soil temperatures and the timing of soil thaw, but had no lasting impact on growing season soil temperatures or hydrology. The considerable variability in the timing of snow release observed between treatments was insufficient to influence the accretion of GDDs, but did have a large effect on the annual number of MJDs to which the communities were exposed.

Although the seasonal trend in average plot greenness was not affected, in most cases, delaying snow melt was found to delay early-season plant phenology. Likewise, for one study species at least, a small advancement in snow release date was found to promote earlier occurrence of initial phenophases. However, reproductive phases were delayed when plants remained snow-free all winter, possibly as a result of frost damage. Temperature related differences in phenology were also observed between plants at the fieldsite and the research station, with more rapid development occurring in the warmer conditions of the latter for all phases except foliar senescence. As in previous studies, plant phenological development was also found to vary naturally between communities and years.

After two years of increased snow cover manipulations at the fieldsite, species/community dependent increases in stem growth and leaf size were observed, as well as individualistic increases and decreases in leaf nutrient content, possibly reflecting snow-mediated modification of nutrient availability as well as direct improvements in protection from harsh winter conditions. Reproductive output was also affected, with species/community dependent decreases observed for the number of flowers produced as well as the quantity and quality of the fruits, probably due to the restriction of the time available for flower/fruit development. As with phenology, these plant performance variables were also found to vary naturally between communities, emphasising the heterogeneous nature of the abiotic environment in the Low Arctic tundra and, at least partly, explaining the variability observed in the vegetation.

In both experiments, increases in snow cover resulted in proportional decreases in carbon turnover, perhaps due to restricted early-season development of the vegetation/soil community and/or indirect modification of carbon and nitrogen availability, but had little influence on NEE. A similar result was observed when all winter snow cover was prevented, this time no doubt, as a result of the increased severity in freeze-thaw regime. Warming on the other hand was found to increase carbon turnover, as demonstrated by the contrast between the monoliths at the fieldsite and those at the research station. Still, this had no effect on net CO_2 balance. However, differences in carbon turnover and NEE were observed between communities at the fieldsite and, as was demonstrated by the modelling exercise, when scaled up temporally, these differences may have a considerable influence on annual CO_2 balance. It was estimated that the three study communities were all net sources of CO_2 to the atmosphere. However, the errors associated with these estimates are large and the modelled plots are not necessarily good representatives of the communities to which they belong. Nevertheless, the exercise did demonstrate that vegetation parameters such as vascular plant cover, growth rate and senescence rate can be important factors in the determination of annual CO_2 balance, while moderate snow-induced changes in growing season length have less of an impact (if the potential influences of associated changes in energy/water balance, nutrient cycling and plant performance are exempted).

Building on the findings of previous studies on snow-ecosystem interactions, the responses of plant phenology, plant performance and ecosystem CO_2 exchange to snow cover perturbation reported here shed a little more light on the nature of the pathways by which snow distribution can influence the structure and functioning of Low Arctic tundra ecosystems. The species specific nature of the phenological and performance-related responses illustrate the numerous ways by which snow cover can influence community composition, while the observed community specificity indicates how snow-plant interactions are dependent on other spatially heterogeneous environmental and genetic factors. Although no major functional responses were observed in terms of carbon balance, it is plausible that the direct responses of plant phenology and plant performance, as well as any resulting compositional and structural shifts, have the potential to modify the role that these ecosystems play, not only in surface exchanges of carbon dioxide, but also of energy and moisture, as well as altering interactions with faunal populations. Structural

shifts could also alter the snow holding capacity of the vegetation, thus providing a direct feedback mechanism by which the ecosystem may influence snow distribution.

Such ecological modification however, involves processes occurring on timescales beyond the short period of this study. To understand them properly requires a greater depth of investigation into the underlying mechanisms responsible for the short-term responses reported here; for instance, what role do snow-induced changes in nutrient cycling play compared with changes in the degree of exposure to adverse winter conditions or variations in growing season length? It also requires analysis of how these mechanisms operate and interact over longer periods of time, how they are modified by shifts in plant/soil community composition and interactions with populations of herbivores and pollinators. More detailed, long-term analysis of snow-ecosystem interactions is therefore necessary if we are to know the true ecological significance of snow distribution. What can be concluded at this point is that the interactions between snow distribution and the Low Arctic tundra plant communities of Northern Fennoscandia are crucial and complex.

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APPENDIX: MODEL DETAILS

1 CALCULATIONS

1.1 Soil Respiration

R_s is given as:

$$R_s = R_{10} e^{308.56\left(\frac{1}{56.02} - \frac{1}{T_s - 227.13}\right)}$$

Equation 1

where R_{10} is the soil respiration rate at 10°C and T_s is the soil temperature (K). Soil respiration is dependent upon the moisture status of the soil as well as its temperature. This is represented in the model by adjusting R_s to zero when soil volumetric water content (θ) is below a community dependent threshold level (θ_{crit}):

$$R_s = R_{s_{wet}} \beta_s$$

Equation 2

where $R_{s_{wet}}$ is the non moisture-limited rate of soil respiration and β_s is the soil moisture factor, which is equal to one when $\theta \geq \theta_{crit}$, and zero when it is below.

1.2 Leaf Respiration

R_d is given as:

$$R_d = V_m F_d$$

Equation 3

where F_d is the dark respiration coefficient for C_3 plants and V_m is the temperature-dependent rate of carboxylation of Rubisco, given as:

$$V_m = \frac{V_{\max} Q_{10}^{0.1(T_c - 25)}}{\left(1 + e^{0.3(T_c - 36)}\right)}$$

Equation 4

where T_c is the canopy temperature (°C), defined as the mean of T_s and air temperature (T_A; K):

$$T_c = \frac{T_s + T_A}{2} - 273.13$$

Equation 5

Q_{10} is the ratio of the rate at one temperature to that at a temperature 10°C lower. V_{max} is the maximum rate of carboxylation of Rubisco (μmol m^{-2} s^{-1}), which is assumed to be linearly dependent on leaf nitrogen concentration, N_l (kg N kg^{-1} C):

$$V_{\max} = N_f N_l$$

Equation 6

where N_f is the constant relating V_{max} to N_l.

1.3 Photosynthesis

W is given as the minimum/most limited of the following three rates:

1) W_C, the potential rate of photosynthesis controlled by Rubisco activity:

$$W_C = V_m \frac{C_i - \Gamma}{C_i + K_C\left(1 + \frac{O_a}{K_O}\right)}$$

Equation 7

where O_a is the atmospheric partial pressure of O_2 (Pa). K_C and K_O are Michaelis-Menten values for CO_2 and O_2 respectively (Pa), given as:

$$K_C = 30 \times 2.1^{0.1(T_c - 25)}$$

Equation 8

$$K_O = 3000 \times 1.2^{0.1(T_c - 25)}$$

Equation 9

Γ is the photorespiration compensation point (Pa), defined for C_3 plants as $O_a/2\tau$ where τ is the Rubisco specificity for CO_2 relative to O_2, given as:

$$\tau = 2600 Q_{10}^{\ 0.1(T_c-25)}$$

Equation 10

C_i is the internal leaf CO_2 concentration, given as:

$$C_i = (C_a - \Gamma) f_0 \left(1 - \frac{dq_{leaf}}{dq_{crit}}\right) + \Gamma$$

Equation 11

where C_a is the atmospheric partial pressure of CO_2 (Pa), given as:

$$C_a = \frac{C_{conc} P}{C_{mix}}$$

Equation 12

where C_{mix} is the CO_2 mixing ratio (kg CO_2 kg air^{-1}), C_{conc} is the atmospheric concentration of CO_2 (kg CO_2 kg air^{-1}) and P is the absolute atmospheric pressure (Pa). f_0 is a constant equal to C_i/C_a when the humidity deficit (dq) is zero. dq is zero when the specific humidity (q; kg H_2O kg air^{-1}) is equal to the saturated specific humidity (q_{sat}; kg H_2O kg air^{-1}). Otherwise it is equal to $q_{sat} - q$, where q_{sat} and q are respectively given as:

$$q_{sat} = \frac{\varepsilon \cdot e_{sat}}{0.001P}$$

Equation 13

$$q = \frac{\varepsilon \cdot e}{0.001P}$$

Equation 14

where ε is the ratio of the molecular weights of water vapour and air, e_{sat} is the saturated vapour pressure (Pa) and e is the actual vapour pressure (Pa), given respectively as:

$$e_{sat} = 0.611e^{\left(\frac{B \cdot T_A}{T_A}\right)}$$

Equation 15

$$e = \frac{RH}{100e_{sat}}$$

Equation 16

where B is the value of wet-bulb depression, set here as a constant, and RH is relative humidity (%). dq_{crit} is the critical humidity deficit and dq_{leaf} is the canopy humidity deficit, given as:

$$dq_{leaf} = \frac{dq}{\left(1 + \frac{r_a}{r_s}\right)}$$

Equation 17

where r_a is the aerodynamic resistance (s m^{-1}) and r_s is the effective surface resistance for the tundra site surface (s m^{-1}) (set here as constants).

2) W_L, the potential rate of photosynthesis dependent upon light and CO_2 availability:

$$W_L = \alpha A_{cr} \frac{C_i - \Gamma}{C_i + 2\Gamma}$$

Equation 18

where α is the quantum efficiency for CO_2 uptake (mol CO_2 mol PAR photons^{-1}) and A_{cr} is the incident photosynthetically active radiation (PAR) in mol PAR photons m^{-2} s^{-1}, given as:

$$A_{cr} = \frac{0.5SW - \Omega}{219000}$$

Equation 19

where Ω is the leaf scattering coefficient for PAR and SW is the incident shortwave radiation (W m^{-2}).

3) W_E, the potential rate of photosynthesis dependent upon the transport of photosynthetic products within the leaf:

$$W_E = 0.5V_m$$

Equation 20

The actual gross rate of photosynthesis, W, is calculated as the smoothed minimum of the three limiting rates above, given by the smallest roots of:

$$\beta_1 W_p^2 - W_p(W_C + W_L) + W_C W_L = 0$$

Equation 21

$$\beta_2 W^2 - W(W_p + W_E) + W_p W_E = 0$$

Equation 22

where W_p is the smoothed minimum of W_C and W_L. β_1 and β_2 are "co-limitation" coefficients.

1.4 Leaf Conductance

Once W and R_d have been calculated, both are adjusted according to whether or not leaf conductance (G_l) exceeds the minimum leaf conductance for H_2O exchange ($G_{l\min}$). $G_{l\min}$ is a constant and G_l is given as:

$$G_l = L\frac{R(T_c + 273.13)(W - R_d)}{C_a - C_i}$$

Equation 23

where L is the ratio of leaf resistance for CO_2 to leaf resistance for H_2O (constant) and R is the universal gas constant (not to be confused with ecosystem respiration). If $G_l < G_{l\min}$, W and R_d are both adjusted to zero. At this point it is also necessary to multiply W by -1, as the value for photosynthesis needs to be negative in accordance with the micrometeorological convention being followed throughout this study.

1.5 Cryptogam Moisture Status

During periods of rainfall, β_{cryp} has a value of one. At all other times it is given as:

$$\beta_{cryp} = \beta_{cryp_{-1}} + D - E$$

Equation 24

where D is dew, which has a value of 0.2 when:

$$T_c + 273.13 - \frac{T_A}{\left(\frac{1 - \ln\left(\frac{e}{e_{sat} T_A}\right)}{B}\right)} < 0$$

Equation 25

Otherwise, D has a value of zero. E is the evaporation rate (kg H_2O m^{-2} hr^{-1}), derived from the Penman-Montieth equation as:

$$E = \frac{\left(\frac{0.0036\Delta(R_n - G) + \rho c_p\left(\frac{e_{sat} - e}{r_a}\right)}{\gamma\left(1 + \frac{r_s}{r_a}\right)}\right)}{\lambda}$$

Equation 26

where R_n is the net radiation flux (W m^{-2}), G is the soil heat flux (as a percentage of R_n) and Δ is the rate of change of e_{sat} with temperature, given as:

$$\Delta = \frac{4098 e_{sat}}{(237.3 + T_c)^2}$$

Equation 27

ρ is the density of air, given as:

$$\rho = \frac{0.003486P}{275 + T_c}$$

Equation 28

γ is the psychrometric constant, given as:

$$\gamma = \frac{0.000001 c_p P}{\lambda \varepsilon}$$

Equation 29

where c_p is the specific heat of air at constant pressure and λ is the latent heat of vaporisation of water, given as:

$$\lambda = 2.501 - (0.002361 T_c)$$

Equation 30

2 PARAMETERS

Table 1: Common state parameters

Name	Description	Unit	Value
B	Wet-bulb depression constant	-	19.65
C_{conc}	Atmospheric concentration of CO_2	kg CO_2 kg air^{-1}	1.5196
C_{mix}	CO_2 mixing ratio	kg CO_2 kg air^{-1}	0.00049
c_p	Specific heat capacity of air	MJ kg^{-1} K^{-1}	1.013
dq_{crit}	Critical humidity deficit	kg H_2O kg air^{-1}	0.15
f_0	C_i/C_a when $dq = 0$	-	0.92
F_d	Dark respiration coefficient	-	0.015
G	Soil heat flux factor	% of R_n	0.05
Gl_{min}	Minimum leaf conductance for H_2O	m s^{-1}	0.000001
L	Ratio of resistance for CO_2 to H_2O	-	1.6
N_f	Constant relating N_l to V_{max}	-	0.0008
N_l	Leaf N content	kg N kg C^{-1}	0.05
O_a	Atmospheric partial pressure of O_2	Pa	20900
Q_{10}	Temperature dependence factor for V_m	-	2
Q_{10}	Temperature dependence factor for τ	-	0.57
R	Universal gas constant	J mol^{-1} K^{-1}	8.316963
r_a	Aerodynamic resistance	s m^{-1}	112
r_s	Surface resistance	s m^{-1}	80
α	Quantum efficiency for CO_2 uptake	mol CO_2 mol PAR photons^{-1}	0.04
β_1	Co-limitation coefficient	-	0.83
β_2	Co-limitation coefficient	-	0.93
ε	Water vapour : air mol. weight ratio	-	0.622
Ω	Leaf scattering coefficient for PAR	-	0.15